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Experiments on Oral* Secretion of the Rocky Mountain Wood Tick, *Dermacentor andersoni* Stiles (Acarina: Ixodidae)[1]

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Tick paralysis continues to be one of the most baffling and fascinating tick-borne diseases in Canada. It was first reported in this country by Todd in 1912. Since then about 250 human cases, including 28 deaths, have been recorded from British Columbia. Outbreaks in cattle have affected up to 400 animals at a time, with losses in a herd as high as 65 head. Although the disease is most common in the Pacific northwest, where it is caused by the Rocky Mountain wood tick, *Dermacentor andersoni* Stiles, it has lately been reported as far south as Florida and has been produced by *Dermacentor variabilis* Say, *Amblyomma maculatum* Koch, and *A. americanum* (L.) (Gregson, 1953). The symptoms include a gradual ascending symmetrical flaccid paralysis. Apparently only man, sheep, cattle, dogs, and buffalo (one known instance) are susceptible, but even these may not necessarily be paralysed.

Attempts to demonstrate the presence of pathogenic organisms by histological methods, by inoculations from paralysed animals, and by placing on healthy animals ticks that have caused paralysis have been unsuccessful. Mechanical injury by the ticks to underlying nerves has been ruled out as the cause as the range in the sites of attachment is wide. Hypersensitivity does not account for the presence of a neuromuscular block which has recently been shown to be present in paralysed animals (Rose and Gregson, 1956). Rather it seems likely that the paralysis is brought about by an injection of a toxin into tissues of the host by the feeding tick.

It was shown (Gregson, 1953) that engorging *D. andersoni* adults, when recently removed from a host, could be induced to secrete an oral fluid into a capillary tube. This is a report on a study of this fluid in view of its probable relation to the production of paralysis in host animals. The technique employed in its collection consists of immobilizing the tick on its back with a wad of plasticine under a binocular microscope. The hypostome and palps are then inserted into an outwardly countersunk hole in a flange of a thin piece of tin, the opening being 1 mm. in diameter. A capillary tube with a 1-mm. bore, previously drawn to provide a 0.4-mm. annealed orifice and calibrated in lambdas (0.001 ml.), is then held by another wad of plasticine and slid over the hypostome of the tick (Fig. 1). The rim of the tapered end serves to push apart the palps, thus further anchoring the tick, and pushing back the soft cheliceral sheath to a position simulating that during the tick's normal attachment to a host.

Secretion, averaging about 7 lambdas, usually takes place within a few minutes after the stimulation, even if the tick has been kept at room temperature for one hour, or on ice for three hours, after removal from the host. It ceases within about 30 minutes, after which the tick may withdraw some or all of the fluid. Dye tests have shown that subsequent small secretions are not of the same

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*The term *oral* is used in a general sense until such time as the exact source of the secretion is known. It is unlikely that the secretion is emitted from the true oral (pharyngeal) aperture.

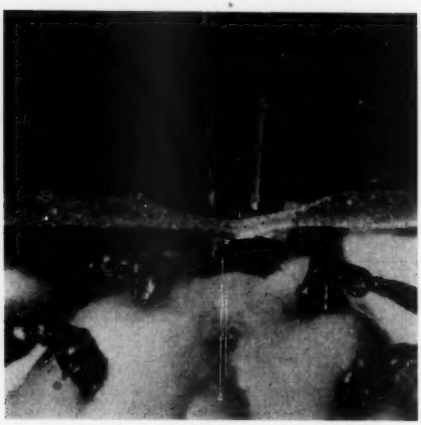

Fig. 1. Positions of glass capillary tube, mouth parts of tick, and flange of tin during collection of secretion.

lot. Similarly, ticks that repeatedly secrete only a fraction of a lambda and withdraw it apparently ingest each portion. Once a tick has reached a peak in its secretion, further substantial secretions cannot be induced, even several hours later, without renewed feeding on a host.

All the following observations and collections were made immediately after the detachment of the ticks. The immobilized specimens were kept under an infra-red lamp at approximately 30°-35°C. To prevent loss of fluid, the capillary tubes were removed from the ticks as soon as its withdrawal became apparent. Secretion before stimulation by the tube occurred rarely and only while a detached portion of the host's skin remained around the mouth parts. This was usually discarded by the tick a few minutes after its removal from the host.

Since it was shown (Gregson, 1944) that mating speeds up the engorging rate of the female, experiments were designed to show whether the secretions from fast-feeding, mated females varied from those of slower-feeding, unmated ones. The female ticks were all placed under capsules on sheep. As a five-day feeding period is apparently necessary for the male before mating takes place (Gregson, 1947), pre-fed males were placed with those females intended for immediate mating. The engorging females, mated and unmated, were then removed at daily intervals in groups of ten for the collection of secretion at different stages of repletion. The secretions and weights of a separate series of 400 randomly mated females were also recorded. Figs. 2, 3, and other data obtained showed that:—

1. The average amount of oral secretion increased as the female tick engorged; the greatest amounts (up to 35 lambdas) came from fast-feeding, mated females between the fifth and sixth days of feeding, when the ticks weighed from 150 to 650 mg.; the greatest amounts from the slow-feeding, unmated ticks were taken between the seventh and eighth days, when the ticks weighed only from 150 to 250 mg.

2. The average amounts secreted by mated and unmated ticks were similar in ticks weighing up to 200 mg.; but larger, mated ticks occasionally secreted more than those that were unmated.

3. The amount secreted by an individual tick, whether mated or unmated, varied widely, especially in the mated group on the sixth day.

4. The variation for individuals was related neither to the size of the tick in the group under observation at the time of secreting nor to its size before feeding. The variation appeared inconsistent, for, on resuming feeding, some ticks that had produced poorly produced abundantly.

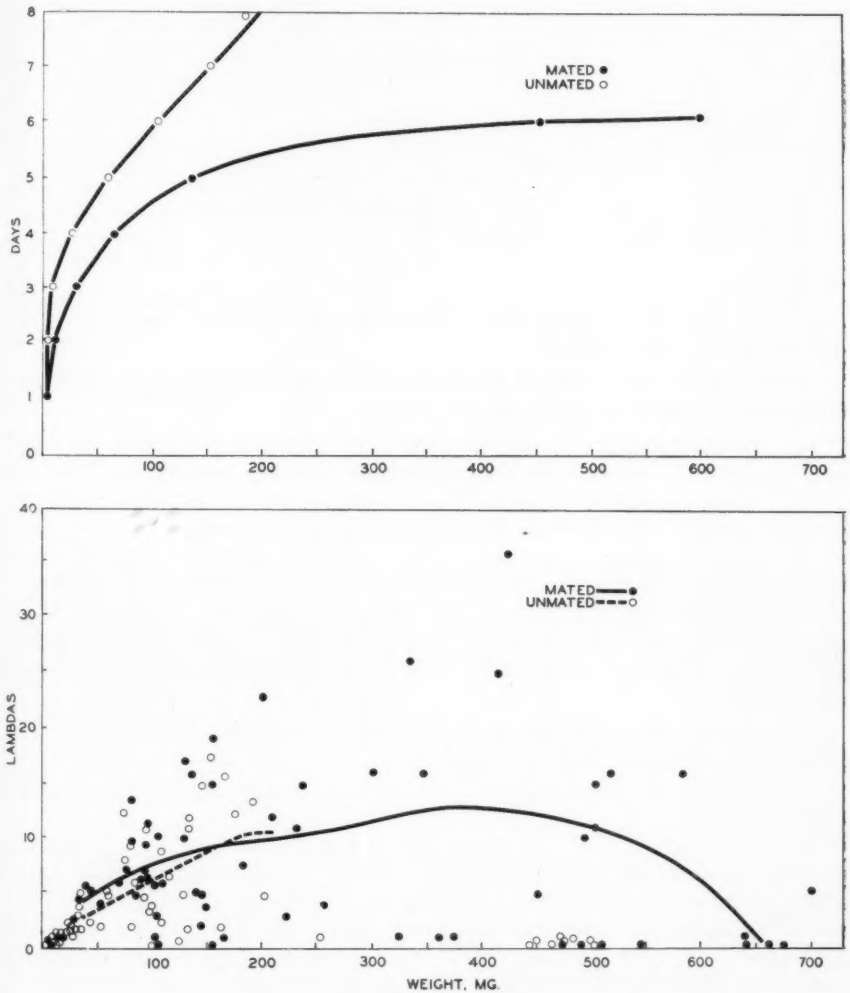

Fig. 2. A. Average weights of engorging mated and unmated females of *D. andersoni* removed from their hosts in groups of ten at daily intervals until either the mated ticks dropped, replete, or the unmated ones had fed for eight days. At the end of 14 days, eight unmated ticks, still attached, had an average weight of 475 mg.

B. Maximum secretions in lambdas (0.001 ml.) of mated and unmated females of *D. andersoni* according to their individual weights before secretion. The ticks were removed from their hosts at random intervals. The approximate length of time that each fed may be estimated by referring to the appropriate curve in A.

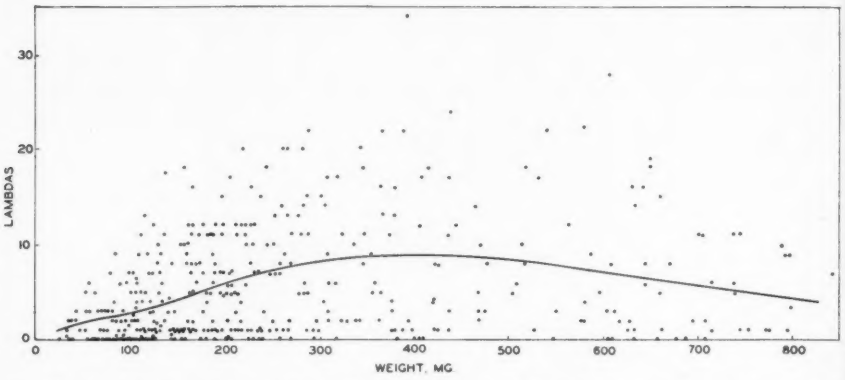

Fig. 3. Maximum secretions of 400 engorging mated females of *D. andersoni* according to their individual weights before secretion.

5. After a tick, mated or unmated, neared repletion, or passed the eighth day of feeding, the secretion usually diminished rapidly, even though the tick was still attached and feeding.

These results are of interest in relation to tick paralysis and suggest that the symptoms are caused by the secretion, since:—

1. Paralysis usually appears only after a tick has been engorging for four or more days. (Tick secretion does not become abundant until then.)

2. There appears to be a variation in the powers of individual ticks to produce paralysis. (Ticks vary in their production of secretion.)

3. Paralysis appears to be produced by either slow-feeding (unmated) ticks or fast-feeding (mated) ones. (These may produce similar amounts of secretion.)

4. Paralysis disappears on removal of the feeding tick, and occasionally even when the tick is still feeding but is near repletion. (Injection of secretion into the host ceases on removal of the tick, and secretion diminishes as ticks near repletion.)

On the assumption that this secretion might contain the causative agent for paralysis, the following tests were made:—

1. 3/10 cc. of pooled secretion (on ice) was injected subcutaneously into a lamb.

2. 1 3/10 cc. of pooled secretion (on ice) from 186 ticks was added progressively to a normal saline solution and allowed to drain subcutaneously into a lamb over a 4-day period, thus simulating the injection of a feeding tick. The rate at which the secretion was introduced slightly exceeded that of the most productive ticks on the successive days of engorgement The dosage was made even more liberal by the fact that ticks can, at their best, only secrete intermittently between intakes of blood.

3. ¼ cc. of pooled secretion (on ice) was injected intravenously into a dog.

4. 1/25 cc. of pooled secretion (freshly collected) was injected intravenously into each of two mice.

5. 1/25 cc. of pooled secretion (freshly collected) was injected intramuscularly into a frog.

6. Seventeen injections and perfusions of freshly collected secretions, along with controls, were tested on frog nerve-muscle preparations.

Not one of these experiments showed any indication of a paralysing agent.

Summary

Tick paralysis is believed to be caused by the injection into the host of a toxin secreted orally by ticks. Observations on the rate, duration, and amounts of secretions produced and collected by the artificial stimulation of the mouth parts of partially fed *Dermacentor andersoni* ticks supported this theory. Attempts to produce paralysis by injecting this secretion into lambs, dogs, mice, and frogs failed.

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The Bark Beetle Complex Associated with Lodgepole Pine Slash in Alberta

Part II—Notes on the Biologies of Several Hymenopterous Parasites[1]

By R. W. Reid[2]

Representatives of the families Braconidae and Pteromalidae were present in association with broods of *Ips pini* Say and *Ips perroti* Sw. The identifications and information on distribution and hosts were kindly supplied by O. Peck and W. R. M. Mason of the Systematic Entomology Unit in Ottawa. Additional information on hosts and distribution were obtained from Hymenoptera of America by Muesebeck, Krombein, Towns, *et al.* (1951).

The following species are discussed: *Coeloides dendroctoni* Cush.; *Pachyceras xylophagorum* Ratz.; *Rhopalicus pulchripennis* Cwf.; *Tomicobia tibialis* Ashm.

Braconidae

Coeloides dendroctoni Cush.

Distribution: B.C. to Calif., east to Mont. and Utah; Quebec.

Hosts: *Dendroctonus monticolae* Hopk.; *D. piceaperda* Hopk., *Ips oregoni* (Eichh.); *I. perturbatus* (Eichh.); *I. emarginatus* (Lec.); *I. vancouveri* Sw.; *Orthotomicus caelatus* (Eichh.).

The biology of this species in Alberta was found to conform fairly closely with that described by De Leon (1935) in his detailed study. Within the experimental area, the period of oviposition extended over three to four weeks following the attack by the *Ips*. In selecting their site for oviposition females moved rapidly over a small area of infested bark, constantly tapping with their antennae upon the bark surface. When a suitable site was found, oviposition took place

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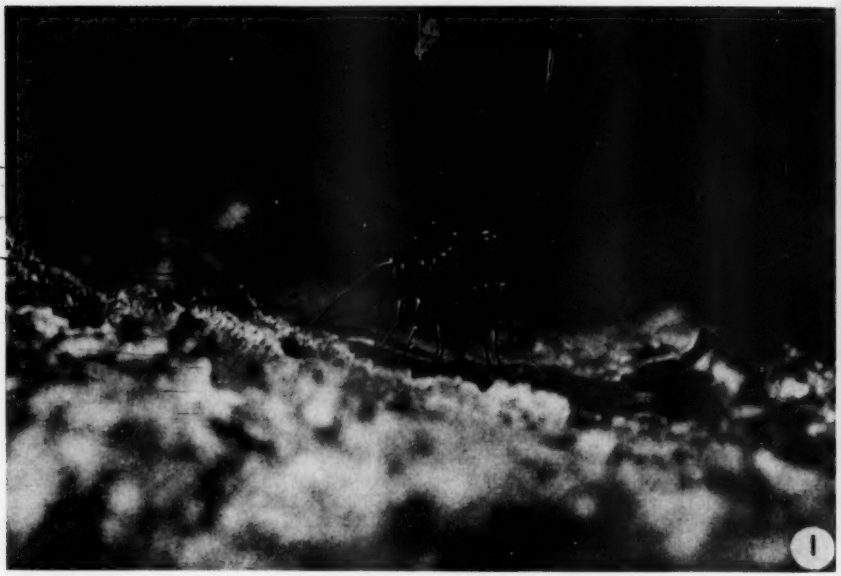

Fig. 1. *Coeloides* female ovipositing through the bark.

through the bark (Fig. 1). The eggs were deposited in the near vicinity of the host. *Coeloides* larvae were observed attached externally with their mouth parts embedded in the host (Fig. 2). They were never found moving independently through the host gallery.

White fragile cocoons up to 6 mms. in length were constructed in the fall by mature larvae. These cocoons were firmly attached to the larval gallery or pupal chamber of the host. Adults emerged the following spring.

Pteromalidae

Pachyceras xylophagorum Ratz.

Distribution. Across Canada; N.H. to N.C., La.

Hosts: *Polygraphus rufipennis* (Kby.); *Scolytus rugulosus* Ratz.; *Ips confusus* (Lec.); possibly *Orthotomicus caelatus* (Eichh.) and *Phloeosinus dentatus* (Say).

The distribution and hosts listed above refer only to North America. A long series of hosts are reported in Europe, where *P. xylophagorum* was originally described.

Adults were found moving over infested slash and ovipositing from late June to early August. Naked pupae were found in the larval galleries and pupal cells of the host. Reared specimens emerged from early August to September. Although the greater proportion appeared to overwinter as adults, some may have overwintered as pupae or larvae.

On occasion, adults were found within the bark-beetle galleries. Only one observation on oviposition was recorded. This female, after searching over a small area arrived within one inch of an entry hole. It entered directly, with no further searching. When the bark was removed, the pteromalid was found well down an egg gallery, ovipositing through an egg-niche plug into the bark-

Fig. 2. Larva of a braconid parasite attached to its host, an *Ips pini* larva.

beetle larval gallery. De Leon (1934) reported similar ovipositing behaviour for *P. eccoptogasteri* Ratz.

Rhopalicus pulchripennis Cwf.

Distribution: Across Canada; Maine, N.H., Md., Mass., N.Y., Mich.; Calif., Wash.

Hosts: *Cylindrocopturus eatoni* Buch., *C. furnissi* Buch., *Dendroctonus monticolae* Hopk., *Ips pini* Say, *Pissodes strobi* Peck; and possibly *Polygraphus rufipennis* (Kby.), *Scolytus piceae* (Sw.), and *Coeloides dendroctoni* Cush.

Adults of this species were found moving over infested slash about the same period as the preceding species. Females oviposited through the bark. Reared specimens emerged from naked pupae in early August and it is probable that their life cycle closely parallels that of Pachyceras.

Taylor (1929) has described the biology of this species, the host in this case being larvae of the white pine weevil, *Pissodes strobi* Peck.

Tomicobia tibialis Ashm.

Distribution: W. Va., N.C., N. Dak., Idaho, Calif.

Hosts: *Ips calligraphus* (Germ.), *I. confusus* (Lec.), *I. grandicollis* (Eichh.), *I. oregoni* (Eichh.), *Ips pini* Say, *Orthotomicus caelatus* (Eichh.), possibly *Pityophthorus puberulus* Lec. and *P. pulchellus* Eichh.

T. tibialis was first observed in the pupal stages within fully mature but dead adults of *Ips pini* and *Ips perroti*. During the spring flight of *Ips*, a small hymenopteron, captured and identified as *T. tibialis*, was observed following an *Ips* adult moving over the bark prior to making its entry hole. The parasite periodically attacked the bark beetle and with great speed and rapid movement of its ovipositor attempted to deposit eggs either on or within the beetle.

In the fall, many of the dead *Ips* adults found in main galleries, the parents of the brood, contained *Tomicobia* pupae each occupying the entire abdominal and thoracic cavities. The pupa overwintered in the host, emerging as an adult in the spring by cutting a round hole through the elytral declivity or posterior ventral portion of the abdomen. No parasites were found in teneral adult *Ips*.

Acknowledgments

Thanks are extended to various members of the Calgary Forest Zoology Laboratory who assisted in the collection of data and preparation of this manuscript. In particular, the aid of G. R. Hopping is gratefully acknowledged.

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Phytophaga rigidae (O.S.) (Diptera: Itonididae), Sawflies (*Euura* sp.) and Hymenopterous Parasites Reared from the Beaked Gall of Willow

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On February 13, 1955, a collection of galls was taken from a row of willow shrubs, *Salix* sp., growing in a ditch on the west side of Adelaide Street between the sixth and seventh Concession lines of London Township, Middlesex County, Ontario. The galls ranged in size from about one inch to one and a half inches long and were fusiform in shape with a slightly curved beak at the tip (Fig. 1, 2, 3). They were identified, with keys and descriptions of galls of willow in Felt (1912, 1940), as beaked willow galls caused by the fly *Phytophaga rigidae* (O.S.). Several galls were split open, disclosing in each a narrow central chamber which was closed at its lower end and which opened at its upper end through the beak. In the chamber was an orange larvae, about 7 mm. long, with its anterior end toward the opening of the chamber. It was recognizable as an itonidid larva because of the presence on it of the "breast-plate" typical of larvae of the family Itonididae.

Method of Rearing

Two hundred galls were clipped from the willow twigs on February 13 and each was put in a separate, numbered, glass vial of dimensions 60 mm. x 15 mm., plugged with cotton. The vials were kept on a rack at room temperature in a laboratory and were examined daily for the presence of insects which had emerged from the galls. The insects were killed, pinned and labelled to show the date of their emergence and the number of the gall from which each insect emerged. The numbers of the various insects that emerged are presented in Table 1. On December 29 all the galls were split open and any insects remaining in them were removed. All the insects are deposited in the collection of the Department of Zoology, University of Western Ontario except some specimens

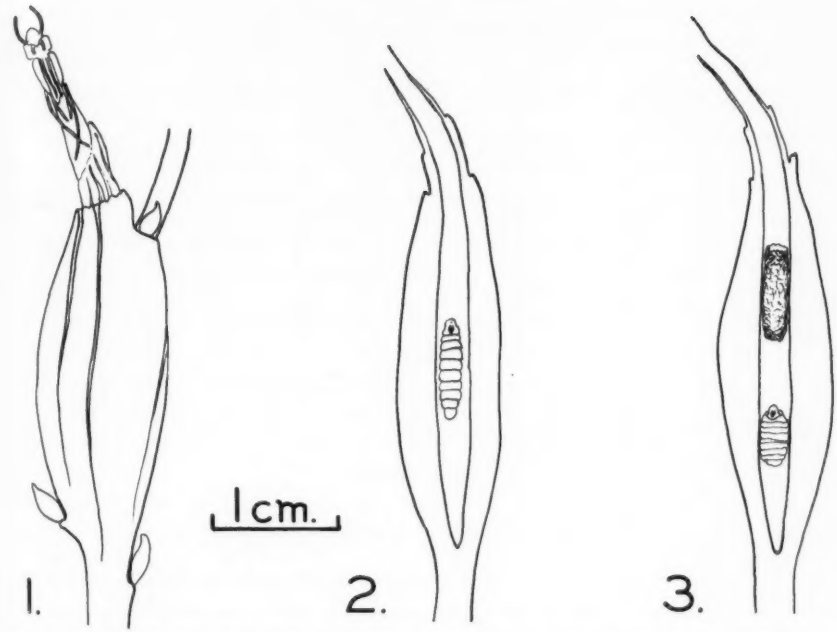

Fig. 1. Beaked Willow Gall with pupal skin of *Phytophaga rigidae* projecting from the beak.
Fig. 2. Longitudinal Section of gall showing larva of *Phytophaga rigidae* in the central chamber.
Fig. 3. Longitudinal Section of gall showing cocoon of *Euura sp.* and, behind it, a shrivelled larva of *Phytophaga rigidae*.

retained in the Canadian National Collection, Ottawa (CNC), as noted in the following account. Of the 200 galls 130 yielded adult *Phytophaga rigidae*, 14 yielded itonidid pupae which failed to produce adults, 15 were found to contain shrivelled itonidid larvae or pupae when split open, 1 was found to contain a sawfly larva and an itonidid larva when split open, 12 yielded adult sawflies (*Euura* sp.), 18 were found to contain no insects when opened and 10 (5%) yielded parasitic wasps.

Account of Insects Reared

Diptera

Itonididae

Phytophaga rigidae (O.S.)

Between February 25 and March 9, 51 male and 79 female *Phytophaga rigidae* emerged from 130 galls (Table 1). Before the emergence of a fly occurred the pupa wriggled out of the chamber to the upper end of the gall; and as the fly emerged it left its empty pupal skin projecting from the tip of the beak (Fig. 1). In addition, 14 pupae wriggled free of the beak and fell to the bottom of the vial and produced no adults. Ten adults are deposited in the CNC.

Hymenoptera

Tenthredinidae

Euura (*salicis-ovulum* (D.T.)?)

Eight adult sawflies, *Euura* (*salicis-ovulum* (D.T.)?), emerged from eight

TABLE 1
Insects reared from Beaked Galls of Willow

Date	Insects Reared									
	Phytophaga rigidae		*Euura* sp.		*Pseudencyrtus cecidomyiae*		*Amblymerus* sp.		*Torymus* sp.	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Feb. 25	6	1								
26	17	10								
27	9	19								
28	9	30								
Mar. 1	1	5								
2	3	5								
3	4	4								
4		2								
5	1	1								
6		1	1							
7	1									
9		1	1							
10				1						
11			1							
16									1	
19										1
23					1	1				
25								1		
27			1							
28								1		
29				1						
30			1							
April 1				1						
2				1						
6									1	
June 4									1	
Sept. 3										1
5										1
Dec. 29 (in gall)			2	1						1
	51	79	7	5	1	1		2	3	4
TOTALS	130		12		2		2		7	

of the galls and three more were found dead in the galls when the galls were opened in December (Table 1). Five of the sawflies are deposited in the CNC. In addition, one female sawfly, *Euura* sp., emerged from a gall on March 29. Muesebeck *et al.* (1951) record that the host of *E. salicis-ovulum* is a stem gall on *Salix humilis*.

When the galls from which the twelve sawflies had emerged were opened it was found that in each gall there was an empty sawfly cocoon toward the open end of the gall, and behind it, a shrivelled though full-grown itonidid larva (Fig. 3). In addition, one gall opened in December contained a dead sawfly larva toward the opening and behind it a shrivelled itonidid larva. The likelihood is that in the case of each of these twelve galls the sawfly larva had crawled into the gall from outside through the beak and entered the chamber, in the fall, thus finding a convenient shelter in which to spin its cocoon.

Encyrtidae

Pseudencyrtus cecidomyiae (Howard)

Two wasps of this species emerged from one gall on March 23 (Table 1). Muesebeck *et al.* (1951) record that its host is *Phytophaga rigidae*.

Pteromalidae

Amblymerus sp.

Two wasps emerged from two galls (Table 1). Both specimens are deposited in the CNC. Muesebeck *et al.* (1951) record that the host of one species of *Amblymerus* is an itonidid gall of willow.

Torymidae

Torymus (*longistigma* Huber?)

Six wasps emerged from six galls and a seventh was found dead in a gall opened in December. Five of the specimens are deposited in the CNC. Huber (1927) records that the host of *T. longistigma* is a woody gall on willow. Thompson (1950) lists several species of *Torymus* (=*Callimome*) as parasites of insect galls and Judd (1953,1955) reared wasps of the genus *Torymus* from willow galls in the vicinity of London.

Acknowledgments

The writer is grateful to Messrs. O. Peck, J. R. Vockeroth and R. Lambert, Systematic Entomology, Department of Agriculture, Ottawa, for identifying, respectively, the wasps, flies and sawflies collected from the galls. The data pertaining to this study were assembled while the writer was holding a Summer Research Associateship of the National Research Council of Canada during the summer of 1956.

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Studies of the Bronze Birch Borer, *Agrilus anxius* Gory, in New Brunswick[1]

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Introduction

Agrilus anxius was described by Gory (1841), and later given the name "bronze birch borer" by Chittenden (1898). It was recently separated from a closely allied species attacking poplar, *A. liragus* (Barter and Brown, 1949; Smith, 1949). The borer is native to North America and occurs apparently throughout most of the range of birch from Newfoundland to British Columbia, and south to New Jersey, Ohio, and Colorado (Barter and Brown, 1949; Fisher, 1928).

Early records on borer injury dealt with widespread damage to ornamental birch, especially the exotic species, in the northern United States and southern Canada from the Great Lakes to the Atlantic Coast (Felt and Bromley, 1930; Gibson, 1909; Jack, 1896; Schwarz, 1890; Swaine, 1915). According to Slingerland (1906) there were no records of injury to forests and woodlands up to that time. The first records of the borer as a forest pest were by Maheux (1919) and Swaine (1918) who reported damage to stands of white birch, *Betula papyrifera* Marsh., and yellow birch, *B. lutea* Michx., along the Ottawa River watershed in 1918; but since about 1925 it has been commonly associated with the dying of birch in forests and woodlands (Hall, 1933; Peirson, 1927; Spaulding and MacAloney, 1931).

What was probably the most severe outbreak in the history of the borer occurred in the late 1930's when most birch trees affected by "dieback" in New Brunswick were being heavily attacked (Balch and Prebble, 1940). Since then the borer has reached outbreak proportions wherever birch dieback has appeared both in Canada and the United States. A numerical idea of the severity of the outbreak in Maine, for example, is obtained from the following statement by Nash *et al.* (1951): "Populations have been high and swarms of beetles have been seen to the extent of counting three hundred from one spot."

Studies on the biology of the bronze birch borer were initiated at Fredericton, N.B. when this insect was found to be closely associated with the "dieback" of birch (Balch and Prebble, 1940). Although the borer had been associated with damage to ornamental trees, relatively little was known of its biology. The results of preliminary investigations on the life-history and habits of the borer were recorded by Balch and Prebble, and some additional conclusions have been given in several reports on the progress of birch dieback and evidence of recovery (Balch, 1944; Barter, 1953). This paper deals with studies undertaken to obtain a more complete picture of the host-insect relationship so that the role of the borer in the dieback complex could be accurately evaluated; it presents the biology of the bronze birch borer in more detail with the addition of information obtained since earlier reports.

Description

Adult

The adult (Fig. 1) is olivaceous-bronze with copper reflections on the pronotum, slender sub-cylindrical, the female being slightly more robust. The length of the females range from 7.7 to 11.3 mm., the males from 6.5 to 9.8 mm. The front of the head of the male is greenish; that of the female is copper-bronze

[1]Contribution No. 336, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

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in colour. The first and second abdominal segments of the male are grooved on the ventral side, the first broadly, the second more deeply.

The adults of *A. liragus* differ from those of *A. anxius* in that the copper reflections are nearly always lacking although sometimes evident near the lateral margins of the pronotum. The males of the two species are separable always by characters of their genitalia (Barter and Brown, 1949). *A. liragus* has 20 chromosomes, *A. anxius* 22 (Smith, 1949).

Egg

The egg (Fig. 2) was first described by Hutchings (1923). The following descriptions are based on some 270 groups collected during this study. Ranging from 1.3 to 1.5 mm. long and 0.8 to 1.0 mm. wide, the egg is oval in outline, much flattened on two sides, creamy white when first laid, later changing to yellowish. After deposition it is coated over by the female with a semi-transparent whitish substance which apparently acts as a protection for the soft shell of the egg during incubation, and as a cement to hold it in place. A parasitized egg first becomes streaked greyish-black, and later turns completely black. The eggs hatch in about two weeks; prior to hatching the young larvae can be seen curled up inside (Fig. 2).

Larva

There are five larval instars. Newly hatched larvae are approximately 2½ mm. long, mature larvae about 1½ inches. All larval instars are nearly white in colour, but when feeding in discoloured cambium acquire a creamy or yellowish brown tint. The larval stages are referred to as "immature", "mature", and "prepupal." The term "immature" applies to instars 1-4; "mature" applies to fifth-instar larvae (Figs. 3, 4). The "prepupal" stage is the shorter, thicker larva (Fig. 5) which precedes development to the pupa (Fig. 6).

The larva (Fig. 3) is typically buprestid, with a wide second thoracic segment and flatter ribbon-like abdominal segments. The caudal segment of all instars terminates in two sclerotized toothed forceps-like prolongations subparallel to the meson, characteristic of the larvae of *Agrilus* (Chittenden, 1898; Peterson, 1953; Slingerland, 1906). The following descriptions are the writer's and include morphological characters not previously recorded. Prothorax with median I-shaped sclerotized line on dorsum, and a similar line, but vaguely sclerotized, on ventrum. Mesothorax and metathorax narrower, shorter, together slightly longer than prothorax and about equal to first abdominal segment. First abdominal segment about as long as broad; segments 2-7 longer than broad, No. 8 shorter than broad. The two caudal segments, the latter tapering, are together shorter than segment No. 8. Two C-shaped spiracles, with slightly pigmented peritremes, occur on the anterior dorso-lateral areas of abdominal segments 1 to 8; slightly larger spiracles not referred to by Peterson (1953), also occur on the mid-lateral areas of the mesothorax.

Pupa

Creamy-white when freshly moulted. Moults from the prepupal stage by wave-like dorsoventral movements which cause the prepupal skin to break on the dorsal side of the head and prothorax, gradually sliding along the body and off the posterior end. As this stage matures, pigmentation commences in the eyes, then the mouth parts; eventually it becomes totally brownish-black.

Life History and Habits

Life Cycle

Differences in length of the life cycle of the borer have been recorded. In the United States Chittenden (1898) and Slingerland (1906) recorded a one-year

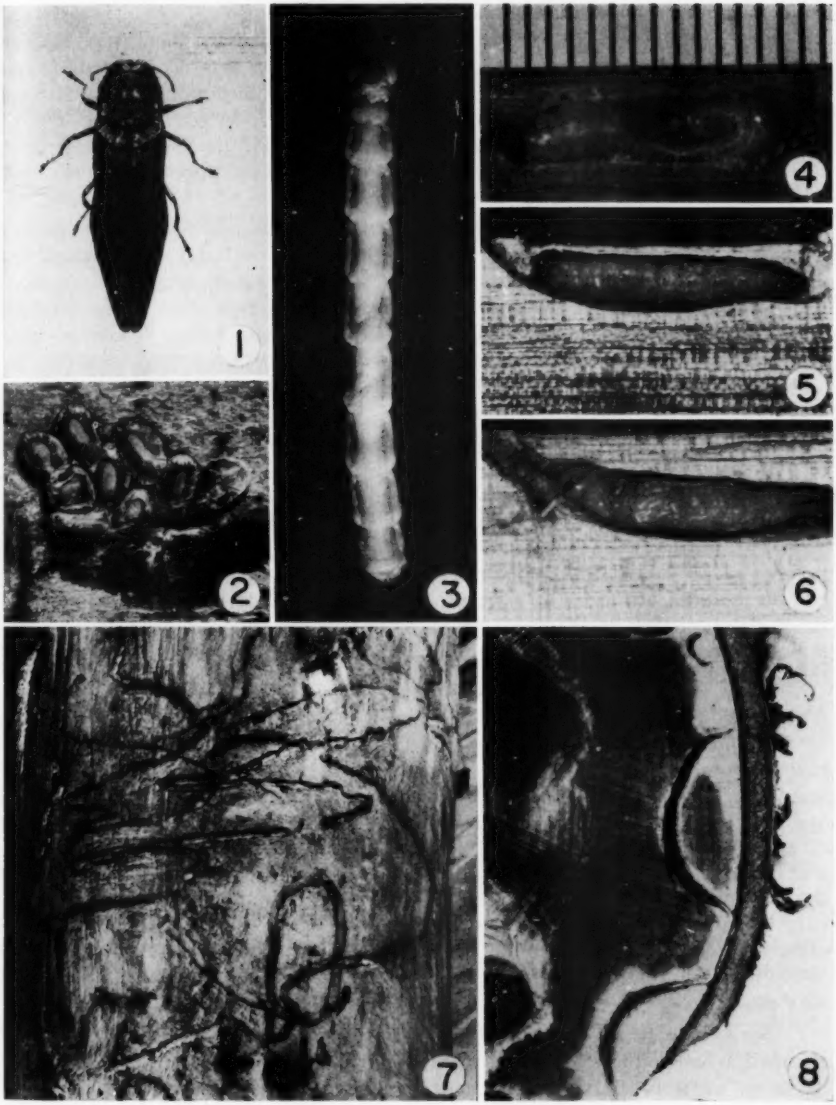
life cycle in New York, and Britton (1923) the same in Connecticut. Hall (1933) and Spaulding and MacAloney (1931) found evidence of a two-year life cycle in New England and the Lake States. Anderson (1944), recorded both a one-year and a two-year life cycle in Minnesota. Nash *et al.* (1951) implied a two-year life cycle for Maine, but noted that development was related to host condition and that some borers may mature in one year. In Quebec, Swaine (1917) suggested that some individuals, at least, require two years to develop. In New Brunswick, Balch and Prebble (1940) indicated a two-year life cycle and expressed some doubt whether the borer could complete its life cycle in one year. They suggested that some individuals may require more than two years to develop.

The effects of geographical location, temperature and time of emergence on development would account for these differences in the length of life cycle. Host condition, as determined by the general health of the tree and condition of the cambial area, and time of egg laying are, however, major factors affecting the life cycle. A two-year life cycle is the general rule in New Brunswick, but, under certain conditions, some larvae can mature in one season, thus completing a life cycle in one year. Rapid development and a one-year life cycle generally results when the cambial tissues become moribund fairly rapidly. On the other hand, in standing girdled trees, which approximate the condition most commonly found by the borer in nature, and where the cambium is more vigorous than in logs, surviving larvae require two years to complete the life cycle. It is only when such trees have been considerably weakened by repeated or heavy attacks, that a one-year life cycle occurs.

Although time of egg laying is a factor in determining the length of the life cycle, it is less important where the breeding material is favourable. In cut logs, larvae hatching from eggs laid as late as the end of July have matured the same year. In such material 32 to 100 per cent and an average of 86 per cent of 375 larvae, from eggs laid throughout the season, completed a one-year life cycle. On the other hand, a similar number of larvae in standing trees weakened by girdling, but with proliferating cambium, required two seasons to mature. Of the larvae hatching from eggs laid in latter trees on July 6, 75 per cent reached the third instar the first year and the remaining 25 per cent developed only to the second instar. From eggs laid one month later, corresponding figures on development were 5 per cent and 85 per cent, with 10 per cent failing to get beyond the first instar. These results are in agreement with those of Anderson (1944) who found that in topped and felled trees a one-year life cycle predominated. "Of the total living populations present when the topped and felled aspen were examined, 83 per cent completed their development in one year." Also, "in trees that were still growing in diameter, very few larvae lived to pupate and the ones that did required at least two years to complete their development."

Emergence and Flight Period

The commencement and duration of the adult emergence and flight period vary with the season. In southern New Brunswick emergence usually commences about June 25 and lasts for approximately 6 weeks, reaching a peak about the middle of July. The flight period extends into August and females have been seen ovipositing as late as the third week of this month. Exceptions to this rule occur when temperatures are unseasonable. In 1949, for example, the weather was quite warm during late April and early May and apparently resulted in a rapid and uniform degree of development of the prepupae. Emergence commenced about June 15, and very few adults were observed in the field after the end of July.



Figs. 1-8. 1, *Agrilus anxius*, adult female; 2, *Agrilus anxius*, eggs (before eclosion); 3, *Agrilus anxius*, larva (mature feeding); 4, *Agrilus anxius*, larva (mature overwintering); 5, *Agrilus anxius*, prepupae; 6, *Agrilus anxius*, pupa; 7, *Agrilus anxius*, larval galleries on surface of xylem. Smaller, partly healed over galleries, were made by immature larvae previous year; larger galleries made by mature larvae present year with no healing; 8, *Agrilus anxius*, larval galleries in and out of xylem. This is common when cambium is too vigorous for developing larvae.

Adult Longevity and Feeding Habits

An average adult life span of 23 days was recorded by Balch and Prebble (1940). In the present study the length of adult life was determined mainly from beetles reared separately in cages in the insectary, although some data were obtained from beetles in oviposition cages in the field. In one series of experiments in the insectary, the adults were deprived of food. In all other tests fresh aspen foliage, kept alive in water in goose-neck vials or other containers, was supplied.

Borer adults require food throughout their life span. Without food they only lived an average of about 4 days or a maximum of 7 days. For those fed in the insectary, the range of life was 13 to 36 days with an average of 24 days. There was no apparent difference in the life span of the two sexes. The life span in oviposition cages in the field did not exceed 16 days, including 6 days of feeding in the insectary, and averaged 12 days. The adults in the field cages usually spent much of their time on sunny days trying to escape and this may have contributed to the shorter life span.

Very few field observations were made on the feeding habits of the adults due to their evasiveness. However, they have been observed feeding on white birch foliage on several occasions during the field season. In cages they show a definite preference for the foliage of poplar, particularly *P. tremuloides*, when given a choice of birch and poplar foliage. They usually fed around the margins of the leaves, but sometimes ate nearly the entire leaf including the mid rib. It is estimated that the average adult will consume one or more average-sized leaves during its lifetime. Observations in the insectary and in the field indicate that newly emerged females feed prior to ovipositing, during which time they become gravid.

Mating and Oviposition

Mating has been observed in nature and in captivity. The time in copula ranged from 3 to 23 minutes, the latter being the exception; the average was 7 minutes. Mating occurred in feeding cages between adults about one day old and at various times during the feeding period of about 6 days prior to stocking of cages. It was also observed in the field during days suitable for oviposition, and it was not uncommon to see adults in copula during the early part of such days before oviposition commenced. Mating has taken place with females that have been ovipositing but this was the exception rather than the rule. Whether more than one mating is required was not determined. However, as many as 25 larvae have been obtained in a cage from a female that was known to have mated only once.

Under laboratory conditions a period of about 6 days is required following emergence before the females show any tendency to lay eggs. Field observations indicated an interval of about one week, during suitable oviposition weather, between the first appearance of adults and oviposition. The favourite place for ovipositing is in crevices beneath loose flakes of the outer layers of the bark, or in cracks in the bark. The female crawls with her extended ovipositor trailing along the surface of the bark, apparently seeking a suitable crevice; when a likely spot has been found she will back up and investigate it with her ovipositor, sometimes from various angles. If the site is suitable she will commence ovipositing and, unless disturbed, will continue to lay eggs until the cavity is filled. During this period the only movements noticeable to the naked eye are the prodding of the ovipositor and occasional slight motions of the pronotum and tarsi, before and after each egg is laid, with a pause during egg deposition. If a small number

of eggs has been laid the female will continue in search of another oviposition site; if a large group has been laid a rest period, which usually takes place on the shady side of the tree, follows.

The length of time spent at one oviposition site varies with the amount of egg laying taking place. A group of 12 eggs is laid in about 10 minutes. The eggs may be laid singly or in groups; as many as 16 eggs have been found in one group, the average number being about 7. The duration of the egg-laying period for an individual was not determined but it appears to last at least several days.

Responses of Ovipositing Beetles

The behaviour of ovipositing beetles and rate of oviposition are evidently governed by temperature, light, and an olfactory response. There is a very definite relation between the air temperature in the shade, the flight of the beetles to the trees, and the length of the oviposition period. No oviposition has been observed when the temperature was below 70°F., in the early morning or late afternoon, or on cool, cloudy, or rainy days. Warm, humid days with temperatures of about 85°F. appear to be ideal for oviposition.

Most of the oviposition takes place on the unshaded part of the tree, which suggests strong positive phototropic response, but experiments have shown that an olfactory response is also involved in the choice of oviposition site. Beetles oviposited on girdled or mechanically-injured trees in preference to uninjured trees, generally choosing the sunny side of the trees and trees most exposed to sunlight. However, when girdled trees were further injured on the shaded or north side by the back of an axe or climbing irons, oviposition occurred on this side or as close to the injured areas as oviposition sites were available. This behaviour indicates that the attraction of sites favourable to the survival of offspring is stronger than the phototropic response. Anderson (1944) found a relationship between amount of tree exposure to sunlight and number of beetles collected in some cases, but concluded that host suitability was more important than the sunlight on the trees.

Sex Ratio and Reproductive Potential

The sex ratio of *A. anxius* was determined from 1056 adults emerging from caged naturally-infested logs. Of this number, 54 per cent were females, indicating approximately a 1 to 1 ratio. The sex ratio of the daily adult flight to trap trees, on days suitable for oviposition, was also observed. The sex ratio for the entire day was about equal, but it varied during the day. The males usually appeared first on the trees, but later in the day when most of the oviposition took place, there were more females than males; towards evening the reverse was the case. In addition to outnumbering the females during the cool part of the day, the males were also more prevalent on cooler days when the temperatures were slightly below the oviposition threshold.

The exact reproductive potential was not determined because of difficulties encountered in obtaining normal or full oviposition, and because only a proportion of the eggs is mature at any time. Dissections of the ovaries of gravid females showed a maximum of 75 mature and immature oocytes, and an average of about 50. Of these, approximately 47 per cent were mature; the remainder ranged from immature eggs to primary oocytes, in the polytropic type of egg tube. If additional oocytes were produced as some of the mature eggs were deposited, this would increase the above determined potential, which is believed to be lower than the actual reproductive potential.

Studies on Larval Habits

The general habits of the larva have been recorded by several authors (Balch and Prebble, 1940; Chittenden, 1898; Hutchings, 1923; Nash *et al.*, 1951; Slingerland, 1906). During the present study larval habits were studied in artificially infested and naturally attacked, uninjured and mechanically injured host material, under the following conditions. Both yellow birch, *Betula lutea* Michx. and white birch, *B. papyrifera* Marsh., trees were used.

Cages approximately three feet long (except where otherwise stated) were placed on the stems of uninjured healthy trees; trees bark-girdled (1-inch wide strip of bark removed) or sap-girdled (bark and xylem cut to about ½ inch depth) at the base, centre, or top of stem; standing topped trees; logs of different lengths; and trees in early to moderate stages of "dieback." Apparently normal branches, on such trees, branches showing symptoms of the malady, and girdled branches on healthy trees were also caged. In some of the cage experiments with a series of cages, on long logs the xylem between each cage on one-half the log was sap-girdled to induce more rapid drying, browning, and death of the cambium, the other half of the log serving as a check. The borer adults used in the cage experiments were fed for about 6 days prior to caging on fresh aspen foliage, and similar foliage was also put in the cage if none was available on the branch or stem. In most cases mating was noted prior to cage stocking. Generally speaking, one female, or a pair of beetles (male and female), gave as large a number of eggs as several pairs of beetles, if not more.

The naturally infested host material in which larval habits were studied included trees in various stages of dieback, and healthy trees with various forms of mechanical injury such as branch girdling, stem girdling (base or top), topped, or cut into logs. During the study it was noted that borer attack was heavier in the girdled trees in one locality than in another, with a corresponding difference in larval development and host deterioration. To determine the relation between population density and development, the local adult population was increased during one season by placing infested adult-producing logs near the injured trees. Experiments were also carried out to determine the effect of fresh cambium on the larva during later instars by transferring second-instar larvae from cut logs to freshly cut logs, and to those cut on the same date from which the larvae were obtained. The techniques of transferring consisted of removing a one-inch square of bark from the log. A suitable V-shaped groove was cut along and across the cambium-xylem surfaces. The larva was placed in the groove, the bark was replaced and held in place with beeswax.

Seasonal Habits

After eclosion the larvae from a group of eggs begin boring through the bark to the cambium layer leaving the shell of the egg packed with fine frass. The remainder of the life of the larva is spent in the feeding gallery between the bark and the wood except for brief periods in the xylem for the purposes of moulting, overwintering, or for a change in feeding conditions (to be discussed later). When feeding has been completed the mature larva constructs an oblong cell either in the xylem, just below the cambium surface, or in thick bark. Before assuming the doubled-up hibernating position (Fig. 4), it prepares an exit up through the wood and bark nearly to the outer surface of the bark, through which the adult later emerges from a D-shaped hole. In the hibernating position most of the ventral surface of the larva is facing the bark so that the adult stage is reached almost with the ventral surface towards the bark and its mouth facing

the bark surface and previously arranged exit. This is the only position from which it can emerge. In some cases the larva becomes turned over before developing to the prepupa (Fig. 5); in such instances the adult invariably dies after feeding a very short distance in the xylem.

All instars are represented in the overwintering larval population. Experiments indicate that only larvae which attain maturity before winter and are later subjected to temperatures below freezing can develop into adults. Immature larvae resume feeding in May, about the time development of the mature larvae is commencing, and when mature prepare their hibernating cells. All larval activity usually ceases by the end of September. Mature larvae overwinter in their cells, in partially completed cells, or in feeding galleries either on the cambium surface or in the wood.

Feeding and Moulting Habits

Larval behaviour is affected by the condition of the host and local feeding conditions in the cambium region. The direction of the feeding larva in standing trees apparently is not governed by positive or negative geotropic response but by the manner in which the feeding area dies. Upon reaching the cambium region the first instar larva commences feeding either diagonally or at right angles across the grain of the wood with most, if not all, of this part of the gallery in the phloem-cambium layer. After a relatively short distance, depending upon the vigour of the host, the larva usually enters the wood either to moult or for a change in feeding conditions, after which it returns to the surface and continues its gallery, between the bark and the wood. If the cambium is quite active, the larva may die. It may survive by sharply reversing the direction of its gallery so that it lies below the previous part of the gallery. This evidently improves its chance of survival since the earlier part of its gallery has a girdling effect, thus interfering with the downward flow of food materials and cambial activity. If the cambial activity is still vigorous when the larva reaches the end of this protective barrier, it may again change its course and in this way a zigzag gallery pattern is formed (Fig. 7) until larval development is complete. In trees which are dying and in which the cambium is inactive or moribund the larva feeds towards fresh tissue, where possible. In standing trees in which the cambium dies first near the roots, and later towards the crown, the feeding larva will usually direct its course upwards. On the other hand if the tree dies back from the top the larval galleries are likely to progress downwards. The latter part of the larval gallery and pupal cell is often found in fresh cambium and xylem on the edge of the browned cambium where the rest of the gallery was formed, as mentioned by Balch and Prebble (1940). In moribund host material the serpentine gallery pattern, with its sharp angles, is much less evident and may extend upwards, downwards, or in an encircling direction around the tree or branch.

During the course of feeding and development, the larvae sometimes work beneath the wood surface at varying intervals. Chapman (1915) working with *A. bilineatus* Weber, found that most entries into the wood were made for the purpose of moulting. Hall (1933) suggested that *A. anxius* larvae entered the wood only for the purpose of moulting, whereas Balch and Prebble (1940) pointed out that many of the larvae go into the wood only once or twice prior to forming the pupal cell, implying that moulting must also occur on the cambium surface since, according to Hutchings (1923), the minimum number of larval instars is five. Anderson (1944) concluded that moulting was the primary reason for entries into the wood, except in less vigorous host material when fewer entries

occurred. In the present study entries into the wood were related to the condition of the host, and particularly to conditions in the cambium layer. In some cases as many as 12 or more entries during larval development have been noted, whereas in other cases no entries were made. Usually, a routine of entering the wood to moult is more closely followed in conditions where the cambium remains living or fresh during larval development than in cases where it becomes moribund and turns brown. The larva moults four times. If feeding conditions suit the normal requirements of each larval instar, entries into the wood are apparently made for moulting only, and each gallery segment becomes progressively longer corresponding to the size of the instar, as also observed by Anderson (1944). In more vigorous cambium, the larvae almost invariably enter the wood to moult but many other entries may also be made (Fig. 8) apparently as a refuge from unfavourable feeding conditions; such entries go deeper into the wood and in some cases may extend to the opposite side of a fairly large branch, an observation which has also been recorded by Larsen (1901). Excessive entries have also been noted where the host became decadent before larval development was complete, although under such conditions most of the moulting occurs on the cambium surface.

Relationship to Host

Host Condition in Relation to Attack

Different opinions have been expressed on the relationship between host condition and attacks of the borer. Balch and Prebble (1940) reported that fewer trees in the early stages of birch dieback were attacked than those more severely affected by the malady. However, they pointed out that the borer was capable of attacking and killing apparently healthy trees. Nash *et al.* (1951) reached similar conclusions. These observations were made under outbreak conditions. The more secondary role attributed to the borer by Anderson (1944), Hall (1933), Hawboldt and Skolko (1948), Quirke (1953), and Spaulding and MacAloney (1931), may be explained by the absence of such outbreak conditions.

During the course of this study the borer demonstrated a secondary tendency, generally speaking, both in cages and in nature. The following injury classes cover the condition of standing host material used in our cage experiments.

1. Crown normal, apparently healthy tree.
2. Crown thin in top, bare twigs; no dead branches.

3A. Several small branches dead.

3B. Less than one-half the crown dead.

4A. More than one-half the crown dead.

Nash *et al.* (1951) encountered difficulties in obtaining borer attack in cages. In their cages on various types of trees—healthy, decrepit, and girdled—"eggs laid were negligible and did not develop." In the present study borer attack was found in 55 per cent of 115 cages. The proportion of cages with attack and degree of attack increased, up to a point, with the moribund state of the host material. Attack was found in 30 percent of the cages on ungirdled trees in Classes 1 to 4, as compared with 82 per cent in the more moribund girdled or topped trees, and logs. Of the cages on Class 1 and 2 trees, 25 per cent showed attack as compared with 33 per cent for those on trees in Classes 3A and 3B. However, there was no apparent intra-class difference in the percentage attacked in the two groupings.

The relationship between attack and cage length was tested on logs with one mated female per cage. In cages 1 foot in length, the average number of

attacks per cage was 3.8; in 1½-foot, 2-foot, and 4-foot cages the averages were 5.5, 9.7, and 17. The best results were obtained in cages when only one mated female or one pair of beetles, at one time, was used. Overcrowding, either by placing too many beetles in a cage, or by too close fitting sleeve cages, had a limiting effect on oviposition.

In nature the borer showed either a secondary or primary tendency. Data on borer attack in sap-girdled trees and ungirdled companion trees (coppice growth) suggest that this was governed mainly by the borer population level. Before the data are discussed, however, some of the effects of sap-girdling (cutting into the xylem about one-half inch) should be mentioned. Sap-girdling, at the base of stem almost invariably induced borer attack. This injury alone kills a tree in about 3 years. Those attacked die in from 1 to 3 years, the rate of deterioration and death being closely related to degree of attack.

Wood growth takes place only above the girdle as long as the tree remains alive; it apparently is not affected much during the season of girdling, either by girdling or attack, but subsequent wood growth is reduced, the rate of which is closely related to attack.

Table 1 shows the degree of borer attack during four seasons (1943-46) in two sap-girdled trees at Acadia Station where the population was low. There was no increase in borer attacks, (53, 39, 28, 45) in Tree No. 238 during the four seasons following girdling, even though the tree was in a moribund state when analysed. The results are somewhat similar in Tree No. 391; attacks in this tree for 1943 and 1944 were 16 and 11. In 1945 the number of attacks increased to 91, which coincided with the emergence of 10 adults resulting from the 1943 attack. No attack occurred in 1946 when only one adult from the 1944 attack emerged.

Although borer attack was found in all girdled trees at Acadia Station, no attack was found in ungirdled companion trees. This was almost invariably the

TABLE 1

Attack, survival, development and mortality of larvae, following girdling, in two healthy white birch trees at Acadia Station which were sap-girdled, at base, June 14, 1943 and analysed September 12, 1946 when dying

Tree No.	Year	Total Attacks	Percentage Surviving	Years to Mature	% Dead (Instars)	
					1st	2nd–4th
	1943	53	0	–	96	4
238	1944	39	0	–	100	0
(5″ D.B.H.)	1945	28	75	2	11	14
	1946	45	64 (1)	1 & 2	0	36
	1943	16	63 (2)	2	31	6
391	1944	11	9	2	91	0
(6″ D.B.H.)	1945	91	38	2	52	10
	1946	0	–	–	–	–

(1) 31% mature, remaining in 2nd–4th instars.
(2) Emerged as adults in 1945.

case at Noonan, in 1944, where subsequent studies were carried out and where a slightly higher borer population was indicated by degree of borer attack in girdled trees (Table 2). In 1945, the local borer population was increased by placing adult-producing logs in the vicinity of girdled trees to determine whether this would result in an increase in borer attack. The following conclusions may be drawn from the data. There was a considerable increase in borer attack in the girdled trees at Noonan in 1945: 5.6 to 12.7 larvae per sq. ft. of bark surface compared with a previous maximum of 3.3 (Table 2, N2, N5, N4, N1). Further, this increase coincided with considerable attack (3.2 to 5.8 larvae per sq. ft.) in the ungirdled companion trees (Table 2, N3, N5). Thus, in addition to an increase in borer attacks in girdled trees, which coincided with a local increase in the borer population, about 45 per cent of the total attacks in girdled and ungirdled companion trees, occurred in the healthy companion trees. Trees girdled in the fall of 1944 (after beetle flight) were more heavily attacked the following year (1945) than those girdled in the spring of 1944, and already subjected to one season's attack (Table 2, N4, N5, N3). These results show that the borer has a preference for injured host material, particularly when the insect population is low; when numerous, it is more aggressive, but the most decadent host material in the stand is not necessarily always the most heavily attacked. Fresh or recent injury appears to be more of an attractant to the borer than older injury; in the case of the former, vigour and sunlight appear to be factors influencing degree of attack.

TABLE 2

Survival, development, and mortality of larvae, in relation to degree of attack, following girdling, in healthy white birch trees, at Acadia Station (A) and Noonan (N), which were sap-girdled at base just before beetle flight.[1] (The borer population was increased at Noonan in 1945 by artificial means)

Series	Year	Attacks per Sq. Ft. Bark Surface	Percentage Surviving	% Mature		% Dead (Instars)		No. Trees
				1st yr.	2nd yr.	1st	2nd–4th	
A1	1943	1.3	7	0	–	93	0	2
N1	1944	3.3	5	0	–	78	17	2
N2	1945	5.6	45	0	–	50	5	4
N4	1945	12.7	83	5	–	9	8	3
N5	1945	7.5	49	0.3	–	49	2	2
N5–ck.	1945	5.8	37	0	–	62	1	2
A2	1943	1.5	25	0	25	63	12	3
	1944	1.4	50	10	–	21	29	3
N3	1944	2.1	23	0	23	65	12	5
	1945	4.3	70	1	–	25	5	5
N3–ck.	1944	0.1	0	0	0	100	0	2
	1945	3.2	22	0	–	75	3	2

[1]N4 & N5 girdled previous fall.

Development and Survival

According to Balch and Prebble (1949), the larvae are "evidently dependent for nutrition during the greater part of their existence on the cambium and the young wood and phloem on either side of it . . . there is some evidence that the maturing larvae cannot reach the prepupal stage in a living branch, although healed-over galleries of three-quarters grown larvae are common in lightly attacked trees which have continued to put on normal growth, and prepupae have been found in the living part of partly dead branches." Nash *et al.* (1951) were in general agreement, but pointed out that, "occasionally, individuals develop fully in apparently normal tissues." Anderson (1944) found that, although trees not growing in diameter were more suitable for larval development, "the cambial tissues had to be alive if the larvae were to complete their development successfully." Chapman (1915) noted that *A. bilineatus*, in oak, developed more slowly and was apt to die in dry wood. Living tissue had a greater nutritive value and was more favoured to rapid and extensive feeding.

Borer larvae may mature in feeding galleries ranging in length from about 10 to about 50 inches, in one or two years. Evidently this wide range of development is largely related to nutritional factors in the cambium region where the larvae do most of their feeding. The larvae thrive better, and follow their regular habits more closely, in living moderately proliferating cambial tissues which cease to proliferate and commence to die as the larvae become mature. Newly hatched larvae, upon reaching the cambium region, usually feed a distance of about 3 inches before moulting to the second instar. If the cambium is too vigorous they die after making a relatively short gallery, particularly if the attack is light. There is no evidence that they enter an "incipient stage", however, awaiting more favourable conditions for development, like the California flat-headed borer *Melanophila californica* Van Dyke, as recorded by West (1947). If the cambium dies and turns brown too rapidly, development is prolonged considerably and mortality is high. Many surviving larvae are unable to moult after making galleries 13, and even 18 inches long. Those that are able to moult do so after feeding about twice the normal distance, or 6 inches. Older larvae, particularly those in the fourth and fifth instar, appear more capable of completing their development in browning cambium; although development may be prolonged. Fresh non-proliferating cambium also prolongs development in the later instars, as suggested by the results of transferring second-instar larvae mentioned earlier. Only 36 per cent of the larvae which were transferred to fresh cambium matured, compared with 100 per cent for those transferred to browning cambium. The galleries of the larvae that matured in fresh cambium were 27 per cent longer than those maturing in browning cambium. In general, early instar larvae appear able to survive more vigorous cambium than those in the later instar.

In caged and uncaged host material, development and survival, generally speaking, were related to feeding conditions, and degree of attack. None of the larvae survived on living branches in classes 1 to 3A on standing ungirdled trees. In most cases they died in the first instar and none developed beyond the second instar. Girdled branches, girdled stems and felled trees were more favourable for development and survival. In these the larvae reached maturity in one or two years, depending on feeding conditions. Some larval mortality occurred in living proliferating cambium, but in most cases it was associated with too-rapid browning of non-proliferating cambium.

The results of long-term cage experiments (Figs. 11, 12) show the relationship between repeated attacks and development and survival in healthy trees. Sleeve-cages 12 feet long were placed on the stem commencing at about 2 feet from the ground. Field-collected female and male adults, no more than three pairs at one time, were placed in the cages at intervals, during the flight period, for three consecutive seasons (1947-49). Foliage was provided as described in previous experiments. The cages were not stocked the fourth season, and when it was evident that tree No. 1 was in a considerably weakened condition, the cage was removed to allow exposure of the entire stem to natural attack. The trees were analysed in the fall of the fourth season (1950). Tree No. 1 (Fig. 12A) was attacked each year during the 4-year period (1947-50) and was in a dying condition when analysed. It was attacked only within the cage the first year. These attacks were unsuccessful, but they were concentrated in the upper part of the caged area practically girdling the stem at that point. In the second season lighter unsuccessful attacks were scattered over most of the tree. In the third season (1949) moderate attacks occurred inside the cage, some of which were successful. In the fourth season, when the cage was removed, light to moderate attacks took place over the entire tree; these were apparently succeeding (no larvae were mature) and the only larval mortality was attributed to browning cambium.

Tree No. 2 (Figs. 11, 12B), one of two trees originating from coppice growth, was unsuccessfully attacked during the three seasons that the cage was stocked. As in the case of Tree No. 1, above, the caged tree was attacked only inside the cage the first season. The following season heavier attacks occurred both within and outside the cage, with a few attacks extending up into the crown. In the third season, attacks over the same general area were very light and none occurred the fourth season (1950) when the cage was not stocked. Its companion (Fig. 12C) was not attacked. These results indicated the secondary tendency of the borer in that it required weakened trees to develop successfully. They also point up the effect that repeated attacks have in bringing about conditions favourable for development and survival.

Somewhat similar results have been obtained in naturally infested sap-girdled and uninjured companion trees. Table 1 shows the results of borer attack in two sap-girdled trees at Acadia Station, where the borer population was light, which were girdled in the spring of 1943 and analysed in the fall of 1946. None of the attacks were successful in tree No, 238 until the third season (1945) and it took two years for the larvae to mature. The fourth season a one-year life cycle took place. Larval survival during the last two seasons amounted to about 75 per cent and 64 per cent respectively. Tree No. 391 was attacked only in the first three (1943-45) of the four seasons. Some of the larvae of each attack survived, even though this tree was less heavily attacked during the first two seasons than No. 238. However, in all cases, the larvae required two seasons to mature. These results are similar to those shown for other trees in the same area (Table 2, A1, A2). On the basis of the following data, it is believed that the degree of attack in these trees was below the threshold affecting development and survival and more favourable conditions for development did not occur until the host became weakened as a result of the girdling rather than borer attack.

The relationship between degree of attack and borer development and survival at the end of 1 and 2 years, is evident in the data from Acadia Station and Noonan shown in Table 2. In the Acadia Station trees, where the borer

population was consistently low, only 7-25 per cent of the larvae survived and none matured the first year (Table 2, A1, A2). At Noonan, in trees with a low borer population, survival and development were somewhat similar (Table 2, N3, N1). However, an increase in degree of attack was accompanied by an improvement in larval survival and development. For example, in trees with 5.6, 7.5 and 12.7 larvae per sq. ft. the percentages surviving were 45, 49, and 83, respectively. Corresponding percentages for those maturing in one year were 0, 0.3, and 5.3 (Table 2, N2, N5, N4). Survival was lower in the uninjured companion trees, but not strikingly so in those with the heavier attacks (Table 2, N3).

The effect of condition of the host on the life cycle and length of the larval galleries is indicated by the fact that larvae maturing in two years made galleries from 30 to 52 inches long; those maturing the second year (in one season only) made galleries 18 to 20 inches long.

Nature of Injury to Tree

All of the borer damage is caused in the larval stage. Long-term cage experiments with white birch, described in the preceding section, have shown that repeated borer attacks can injure or kill healthy trees. Injury is caused by the larval feeding galleries which run in a serpentine manner between the bark and the wood, producing a girdling effect upon the branch or stem. The amount of injury is related to distribution and degree of attack. Since borer-attacked trees show injury similar to that produced in mechanical girdling experiments (to be discussed later), it is postulated that the larval galleries interfere with the normal translocation of food materials which, as apparently shown by Curtis

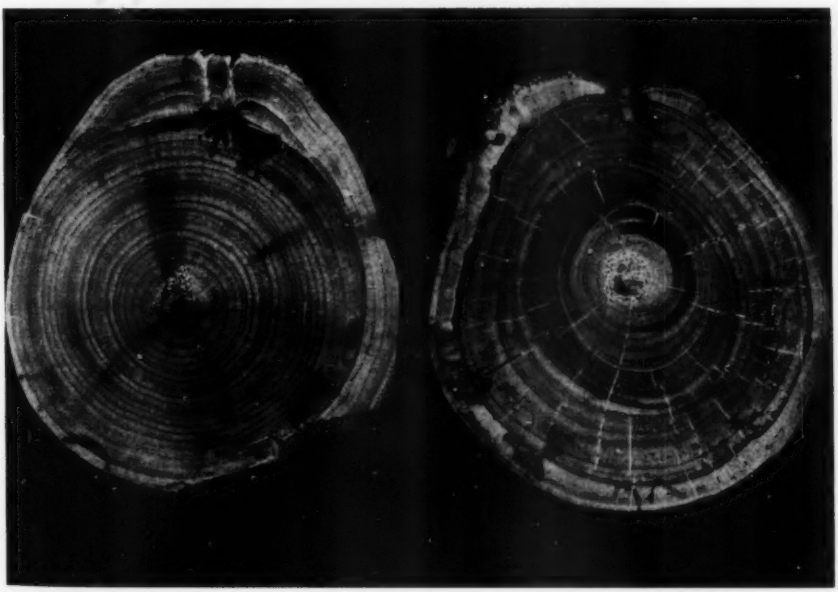


Fig. 9. Sections of young white birch tree showing healing of injury caused by unsuccessful bronze birch borer attack. (Arrow above points to injury from borer gallery; that below to injury not healed over).

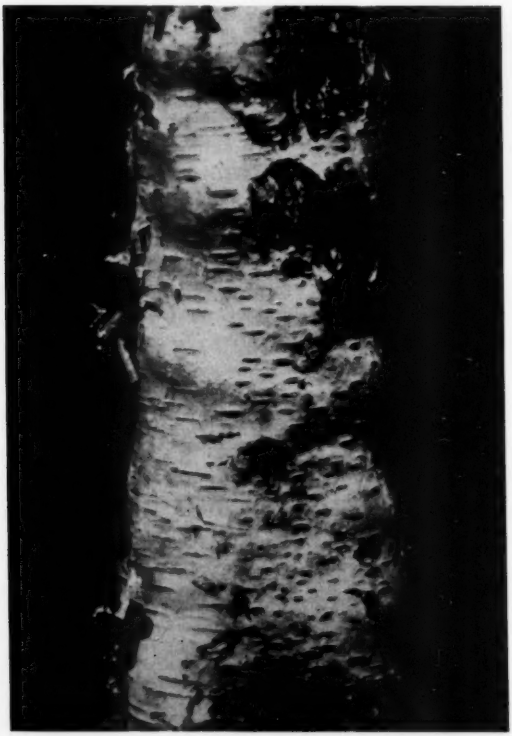


Fig. 10. Swellings on stem of young white birch tree due to healing of unsuccessful attack 8 years previous.

(1935), occurs principally through the phloem in both an upward and downward direction.

In trees which survive borer attack, the larval galleries become healed over by callus growth (Fig. 9). This healing becomes apparent the year after the galleries are commenced. If the tree is lightly attacked the galleries become healed over in one or two years. In some cases as long as ten years may be required to heal over the borer injury (Balch and Prebble, 1940). This is the exception rather than the rule, and applies mostly to trees low in vigour or fairly heavily or repeatedly attacked, and when larvae reach fairly late stage or cause wide galleries. Trees surviving borer attack are fairly conspicuous in a stand because of the swellings caused in the healing process (Fig. 10). Injury to the crowns of such trees may be in proportion to the amount of healed-over attack, particularly in stands where there has been a recent outbreak of the borer (Barter and Cameron, 1955). Some trees with old, healed-over attack appear to be as healthy as those unattacked, indicating that recovery from borer attack is possible.

Foliage Symptoms

Tree No. 1 (Fig. 12A) was attacked by the borer during four successive seasons (1947-50). Although it remained sparsely foliaged until normal leaf-fall

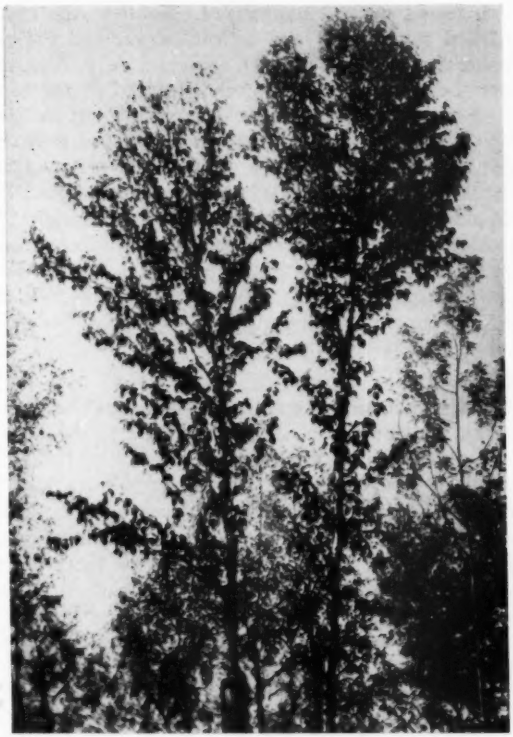


Fig. 11. White birch trees No. 2 and 3 used in long-term cage experiments. Caged tree on left unsuccessfully attacked by the borer during the three years 1947-49; check tree on right was unattacked. Both trees previously had identical crowns. (Note dying back of upper crown and more densely foliated lower crown of attacked tree, which followed attack).

in 1950, the condition of the cambium when the tree was analysed suggested that it would not have survived another year. The foliage became slightly chlorotic on the upper part of the crown by the end of the summer of the first year's attack (1947) but there were no bare twigs. In 1948 bare twigs were evident on the lower one-half of the crown and the amount and size of the foliage was considerably reduced; chlorosis was more marked than it was the previous season. This coincided with light to moderate attack over the entire tree, and followed moderate attack the previous year (inside the cage only) which practically girdled the stem at one point, near the base of the crown. It is believed that this was responsible in part for the bare twigs on the lower part of the crown. During 1949 and 1950 the reduction in the amount and size of foliage was gradual and fairly general over the whole crown, not from the tip downwards as in Tree No. 2 (Figs. 11, 12A), with marked chlorosis commencing near the end of the summer.

The foliage on Tree No. 2, which was unsuccessfully attacked during three seasons (1947-49), also showed evidence of injury the first season. By September, 1947, it became slightly chlorotic over the whole crown, particularly the top,

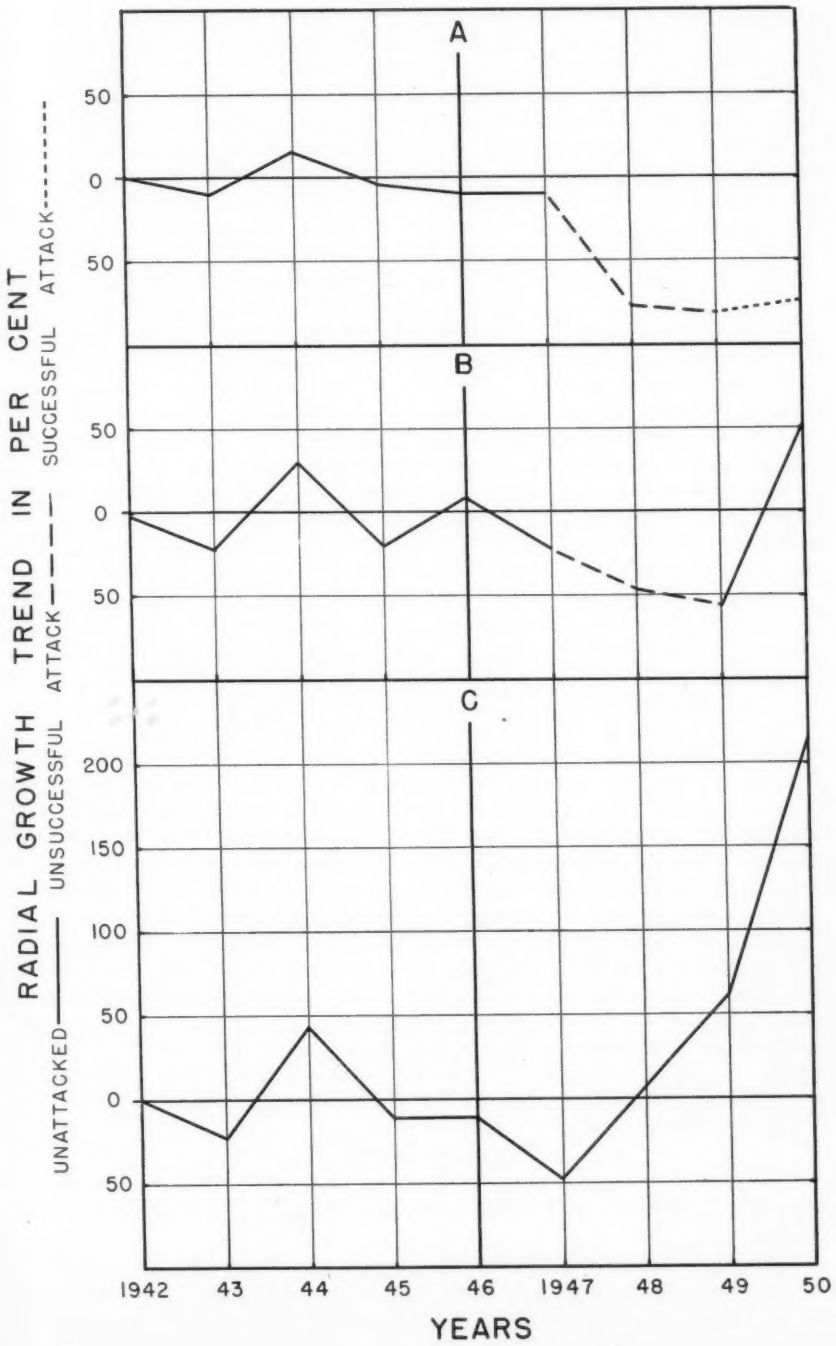
whereas the check tree remained unchanged. In 1948 the chlorotic condition became more marked toward the end of the season and the foliage was conspicuously undersize at the top of the crown. Very few bare twigs were apparent, however, but adventitious growth appeared at the base of the crown and upper stem. Although a disturbance became evident in 1947 when moderately severe attacks occurred inside the cage only, marked injury did not become evident until 1949, the year after heaviest attack occurred over the whole length of the tree. Attack the third season (1949) was very light. Deterioration of the upper crown continued the fourth season, even though the tree was not attacked, but no chlorosis was evident. However, this loss of foliage in the upper crown was offset by an increase in the amount of adventitious growth on the lower crown and upper stem (Fig. 11). Both this tree and its check had identical crowns when the experiment was started, but attacks by the borer changed this considerably, as is evident in the figure.

Annual Radial Growth

Borer attacks, whether unsuccessful or successful, have an effect on the annual radial growth, the amount of which is related to the degree and distribution of attack. This reduction becomes apparent the year following initial attack (Fig. 12) since about 50 per cent of the annual radial growth, which takes place over a period of about three months (June-August), has occurred by the time the first newly-hatched larvae reach the phloem-cambium layers. The radial growth data in Fig. 12 (A-C), were obtained from the three healthy white birch trees used in long-term cage experiments referred to earlier. They are based on the average of four radii at three levels (base, centre, and top) in the stem. The growth trend is the deviation from a 5-year average (1942-1946) immediately preceding caging. All trees were carefully examined for borer attack prior to or following the 1947 caging when cut in the fall of 1950. Tree A, which was growing singly, was in a dying condition due to partially successful borer attack, during the 4-year period 1947-50; B was unsuccessfully attacked during the 3-year period 1947-49, whereas its companion C remained unattacked.

It is seen that growth reduction attributable to borer attack first occurred in 1948, the year following initial borer attack (Fig. 12, A-C). At that time the successfully attacked tree (A) suffered the greatest loss of growth, 76 per cent as compared with 46 per cent for B. Although it was only slightly more heavily attacked in 1947 than B, the attacks were concentrated near the upper part of the caged area, thus causing a more complete girdling effect, which may have been mainly responsible for the greater growth loss and success of later attacks. The growth trend continued downward in 1949. Although a slight increase is shown for 1950, this was comprised entirely of excess callus growth on the upper stem, the only growth occurring that year. In the unsuccessfully attacked tree (B), growth reduction amounting to 46 and 47 per cent, respectively, occurred in 1948 and 1949 only. This followed fairly well-distributed light to moderate attack inside the cage in 1947, moderate attack and light attack over the entire tree in 1948. In 1950 the radial growth was above normal rate, following the tapering off of attack in 1949 and no subsequent attack (Fig. 12, B). Radial growth increased rapidly in 1950 in the unattacked tree (Fig. 12, C). Since

Fig. 12. Radial growth trend of three healthy white birch trees used in 1947-50 cage experiments. (A) caged, attacked over the 4-year period, becoming successfully attacked last two years. (B) caged, unsuccessfully attacked 1947-49, unattacked 1950. (C) uncaged, unattacked "companion" of B (Fig. 11). (Growth based on average of 4-radii in sections from base, centre, and top of stem; trend is based on 5-year period, 1942-46, prior to caging).


A
B
C
50
0
50
50
0
50
200
150
100
50
0
50
RADIAL GROWTH TREND IN PER CENT
UNATTACKED —— UNSUCCESSFUL ATTACK — — — SUCCESSFUL ATTACK ·····
1942
43
44
45
46
1947
48
49
50
YEARS

both B and C occupied part of the same root system, it may be that the unsuccessful attack in the former favoured growth in the latter in 1949 and more strikingly in 1950 (Fig. 12, B, C).

The data for the unsuccessfully attacked tree showed that radial growth was reduced more in the base of the stem, less in the centre and least in the top. When recovery commenced in 1950 the picture reversed. This behaviour was less striking in the successfully attacked tree, in which attack was less evenly distributed.

Some Effects of Girdling

Various bark-girdling experiments were carried out on apparently healthy yellow and white birch trees to determine the effects of different types and degrees of mechanical injury, and their relationship to trees affected by "dieback" and/or attacks by the bronze birch borer. The girdling was mostly done during June and July, and ranged from fatally severe (removal of the bark from the stem, below the crown) to temporary injury (saw-cuts, to simulate borer galleries, on a branch or branches of the main crown). In a few cases, with young yellow birch trees, narrow stem girdles (¼″ to 2″) were covered with paraffin wax, and taped with electric tape, to prevent drying of the cambium. In addition a few trees were pruned severely by removing about one-half to two-thirds of the number of main branches from the crown. No attempts were made to protect the treated trees from borer attack. Some of the young girdled trees were in an area relatively free from adult-producing host material, however.

It was evident from the data that there must be a continuous linkage between the foliage and the root system, through the phloem, if a branch or tree is to remain alive. Girdles wider than ⅜″ were not noted to heal over, and the closer the girdles were to the foliaged part of the stem or branches, and the wider the girdle, the more severe the resulting injury. The foliage may be affected during the season of girdling, but this depends upon the time of girdling and mainly upon the width and location of the girdle. In cases of temporary injury, narrow girdles which are later bridged, the foliage is affected until the wound becomes healed. Annual ring growth occurs above the girdle, as long as foliage persists, but none takes place below unless it is bridged. Unless ring growth occurs in a continuous linkage between the foliage and the roots, the branch or tree is adversely affected; if this disturbance is prolonged, death invariably results.

Injury, caused by bronze birch borer attacks, to the foliage and radial growth is not unlike that produced by mechanical girdling. This suggests a girdling effect by the borer galleries, thus interfering with the translocation of food materials between the foliage and roots, through the phloem, which is necessary to maintain foliage growth and tree life. The heavier the borer attack, and the more often repeated, the more complete the girdling effect and resulting damage. In effect, therefore, unsuccessful borer attack is similar to mechanical girdles which are bridged, whereas heavy and repeated attacks compare with unbridged girdles.

Natural Control

The abundance of the bronze birch borer is apparently controlled in part by parasites and predators, but chiefly by host condition and amount of suitable host material.

Slingerland (1906) and Britton (1923) reared a small Hymenopterous parasite *Phasgonophora sulcata* Westw., from the borer. Hutchings (1923) suggested that this parasite was undoubtedly the greatest controlling agent. He stated that "there are also several species of Siricidae (horntails) which attack the larva" and

also suggested that birds may play an important part in control. Swaine (1917) considered parasites important. Balch and Prebble (1940) reared a Braconid (*Spathius* sp.) from the borer and found evidence of parasitism by another undetermined species, but indicated that the percentage of larvae attacked by parasites had been small. Anderson (1944) reared *P. sulcata* from cells of the borer. Nash *et al.* (1951) recorded the most impressive list of parasites of the borer to date. This included two species of egg parasites, one being *Thysanus* sp. and the other a new genus and new species of the family Encyrtidae, and the following eight species of larval parasites: *Atanycolus* n. sp., (probably *A. charus* (Riley)), *Spathius simillimus* Ashm., *Phasgonophora sulcata* Westw., *Doryctes atripes* (Prov.), *Ichneumon* sp., *Glypta* sp., *Pimplopterus* sp., and *Olesicampe* sp. The first three species of larval parasites, listed in order of importance, were the most consistently found, the others only occasionally.

Egg Parasitism

During this study egg parasitism was the highest and most consistent mortality factor directly affecting the borer population. A new species of *Thysanus* and an undetermined species of the family Encyrtidae, possibly of the genus *Coccidencyrtus* were reared. Parasitism over a 5-year period varied from year to year and averaged around 55 per cent. About 5 percent of the eggs failed to hatch, bringing the total egg mortality to about 60 per cent. Parasitism is related to the size of the egg group and exposure to the parasites; large groups of eggs, and those least exposed, usually have a lower percentage of parasitism. In most cases only one of the two species parasitizes the same egg group. *Thysanus* is the smaller of the two species and as many as three adult parasites have emerged from one egg, compared with a consistent one adult per egg for *Coccidencyrtus*. This difference between the habits of the two parasites is usually, but not always, reflected in the percentage of parasitism as shown in the following synopsis for 75 groups of eggs collected in 1946, and in 1947, at Noonan, and Acadia Station.

Noonan

Species of Parasite	% of Groups Parasitized		% Parasitism per Group		% of Total Eggs Parasitized	
	1946	1947	1946	1947	1946	1947
Thysanus	57	50	60	78	28	39
Coccidencyrtus	32	50	71	62	24	31
Both spp.	14	–	64	–	13	–

Acadia Station

Species of Parasite	% of Groups Parasitized		% Parasitism per Group		% of Total Eggs Parasitized	
	1946	1947	1946	1947	1946	1947
Thysanus	–	31	–	49	–	11
Coccidencyrtus	–	56	–	64	–	41
Both spp.	–	13	–	67	–	8

Nash *et al.* reported egg parasitism at Salem and Eustis, Maine, for three consecutive seasons at 49, 49, and 54 per cent; twelve per cent of the 54 were parasitized by *Thysanus* sp.

Field observations indicate that the egg parasites are active during the daily oviposition period of the beetles, and in some cases, at least, they follow the ovipositing females very closely; on several occasions during the collection of female beetles both the parasite and beetle were captured in the same collection vial. Parasites have also been observed investigating likely oviposition crevices or sites which female adults had been examining, or in which eggs were known to have been laid.

The degree of parasitism was not determined outside the study area, but parasitism was noted wherever eggs were examined and is believed to be a common mortality factor of general occurrence or "widespread." Both species have been recovered from the Cascapedia River area in Quebec. Only *Coccidencyrtus* was recovered from eggs collected near North Bay, Ontario, where the parasitism of nine egg groups amounted to 54 per cent.

Larval Parasitism

Five species of larval parasites have been obtained from larvae or prepupae in logs and standing trees in New Brunswick. In order of importance, they are as follows: *Atanycolus charus* (Riley); *Phasgonophora sulcata* Westw.; *Helconidea ligator* (Say); *Spathius* sp.; and *Ephialtes* sp. The first two were recovered frequently, the others only occasionally. Parasitism by *A. charus*, among 600 larvae, ranged from 1 to 52 per cent with an average of 14 per cent. Parasitism by *P. sulcata* in a similar number of larvae ranged from 1 to 8 per cent and averaged 4 per cent. Of all larvae sampled for parasite recovery only 9 per cent were parasitized.

A. charus and *P. sulcata* were the only larval parasites observed in flight in the field. *A. charus* emerges about the same time as *Ephialtes* sp., and is active in the field from early June (about three weeks before borer emergence) until about mid-July. It is active when the larval population consists mainly of overwintering larvae which have resumed feeding to complete their development. *A. charus* probably attacks the overwintering borer larvae since very few of the current season's larvae are available at that time; moreover this parasite has not been taken from trees producing a one-year life cycle of the borer.

On the other hand, *P. sulcata*, has been taken from trees producing a one-year life cycle; it appears in the field about mid-July and is active during July and part of August. Although overwintering larvae are available for attack at this time, the only locations where this parasite was observed in the act of ovipositing were crevices in which borer eggs had been laid and the young larvae had either just hatched or were about to do so.

Woodpeckers

A number of investigators have included woodpeckers and other birds in their records on control of the borer, and some regard these as important in natural control. Hutchings (1923) found birds an important control factor. Balch and Prebble (1940) reported that woodpeckers take a small number of the prepupae from the bark. Anderson (1944) found that about 10 per cent of the prepupae were removed from infested trees left in the woods over winter. Nash *et al.* (1951) pointed out that predation by woodpeckers varied greatly, from very little in some areas to as high as 30 per cent. Analyses of individual trees, by the writer, have shown that up to 51 per cent of the overwintering mature

larvae and prepupae were removed from their cells by woodpeckers. Most, if not all, of this is apparently done in the spring when transformation of the mature doubled-up borer larva to the shortened prepupal stage is occurring. Predation also appears to be more prevalent in the heavily infested trees.

Host Condition

Although parasites and predators are undoubtedly of value in reducing the borer population, previous discussion on development and survival suggests that host condition plays an important part by affecting larval development and the life cycle. Since the borer prefers weakened host material, healthy trees are less likely to become attacked; if attacked, as sometimes happens particularly under population pressure, the attacks are almost invariably unsuccessful unless they are heavy and repeated, as has been demonstrated by cage experiments (Figs. 11, 12). On the other hand, too rapid dying of the host adversely affects development and results in larval mortality. Some striking evidence of this was observed during studies on the role of the borer in "dieback"; in a number of cases considerable larval mortality resulted from rapid browning of the cambium.

Since the borer can only multiply to any extent in trees or in parts of trees that are weakened or dying, its capacity to increase to a harmful degree is limited by the amount of such material in the stand. It has multiplied when many trees have become injured by such causes as 'dieback', cutting operations, or defoliation, and appears capable of responding fairly rapidly to increase of suitable food. "Outbreaks" follow such catastrophic influences on birch vigour and result in the further weakening of trees by 'unsuccessful' attacks which may produce more favourable breeding material but the capacity to kill healthy trees is strictly limited.

This supports previous conclusions that the borer played a secondary role in mortality known as dieback (Balch and Prebble, 1940; Barter, 1953) but indicates that the insect may have been a determining factor in death or recovery of trees.

Artificial Control

The dependence of the borer on weakened breeding material indicates that control must be based on maintenance of the vigour of birch by good silvicultural management (Balch and Prebble, 1940; Hall, 1933; Pierson, 1927). Chemical control can only be justified for the protection of valuable trees during a temporary period of susceptibility due to such influences as defoliation by insects, drought or other disturbances. It is doubtful whether it can be applied profitably to forest stands in Canada although Nash *et al.* (1951) reported that spraying white birch stands resulted in an improvement in their condition. The protection of shade trees, however, is often called for and will be justified if accompanied by measures to increase their vigour and resistance.

The only stage likely to be affected by insecticides is the adult. It must be prevented from ovipositing and the relatively long period of activity calls for an insecticide with residual effects, or repeated application, or a combination of the two. It may be killed by contact, by feeding on sprayed foliage, or by crawling over sprayed surfaces.

Laboratory experiments by the writer showed that DDT had good residual effects on the female adults. Those used were about 4 days old and had been fed on fresh aspen foliage from the time of emergence until the start of the experiments. In one series of experiments the adults were placed in lantern globes on fresh aspen foliage which was sprayed with DDT (50 per cent wettable) at the rate of 1 pound per 100 gallons of water. In the second series,

TABLE 3
Summary of results of spraying sap-girdled white birch trees with DDT to prevent birch borer attack

Formulations	DDT (lb.) per 100 gals.	No. of Applications	% of Trees with Attack	Galleries per Tree	No. of Trees
50% DDT W.P. 1 pt. raw linseed oil per 100 gals. as a sticker	5	2	33	3	9
"	10	1	20	6	5
		2	0	0	10
		3	0	0	10
		4	0	0	6
DDT oil emulsion	5	1	20	3	5
		2	18	2	11
		3	9	1	11
		4	17	1	6
Check trees	–	–	91	37	22

similar adults were placed in lantern globes, without foliage, the inner surfaces of which had been sprayed with this insecticide at ½, 1, and 2 pounds. Some adults were removed from each experiment after exposures of ½, 1, and 1½ hrs., and placed on fresh foliage in clean lantern globes. Their reactions were then observed for a three-hour period, then examined after 9 and 12-hour intervals until dead. Controls were used.

The results of the laboratory experiments showed that DDT will kill the borer adults. Death was not immediate and detrimental effects did not become apparent until at least one-half hour after contact with the strongest concentration (2 pounds), and up to three hours with the weakest (½ pound). This was evident from the erratic manner in which the adults crawled about. As they became more unsteady, some fell over on their backs and were unable to regain an upright position. Fifteen hours after exposure practically all the beetles were lying on their backs, although alive, and death occurred in from 24 to 48 hours. None of the above symptoms, nor any mortality, occurred in the controls.

Field experiments were carried out in a young white birch stand by spraying groups of sap-girdled trees and comparing the amount of subsequent attack with that of unsprayed girdled trees (Smith and Barter, 1951). The girdling was done immediately before the first spray application, about one week prior to commencement of adult emergence. The treatments and results are shown in Table 3. The foliage, branches, and trunks were thoroughly sprayed using a No. 99 Hardie power sprayer. The applications were spaced at approximately two to three-week intervals.

The results indicate that satisfactory protection can be obtained with two thorough applications of DDT at not less than 5, and preferably 10, pounds actual DDT in suspension or emulsion. The first application should be made just before borer emergence, and the second about three weeks later.

Summary

Studies near Fredericton during the years 1941-50 provided information on the life history, habits, natural control, and the interrelations of the borer and the tree.

The adult and immature stages are described.

The borer has a one or a two-year life cycle, mostly the latter. The length of the life cycle is governed mainly by host condition but also by the time of egg laying.

Adult emergence commences about June 25 and lasts approximately six weeks, reaching a peak about the middle of July. The flight period lasts until about the end of August. Oviposition occurs only during rain-free weather with temperatures of 70°F. and above. The eggs are deposited under loose layers of bark, or in cracks in the bark. Most of the eggs are laid on the sunny side of the tree, indicating a photo-tropic response, but an olfactory response determines the choice of host and location of tree or parts of trees.

There are five larval instars. Moulting occurs on the cambium surface or in the wood depending upon the host condition. The larva makes its gallery between the bark and the wood and may enter the wood at different times during development either for the purpose of moulting, as an escape from unsuitable feeding conditions in the cambium, or hibernation.

The larvae cannot survive in healthy trees. Successful larval development is dependent upon the host being in a weakened condition from repeated unsuccessful attack or other injury, such as defoliation by the forest tent caterpillar, adverse weather conditions, or old age.

Borer injury to healthy trees is caused by the larval galleries even though the larvae may not survive. These tend to girdle the cambium and phloem. If the attack is light the galleries are usually healed over with only temporary injury resulting. If the attack is heavy or repeated, the galleries are less likely to be bridged and the continued girdling effect results in the death of the branch or tree.

Two species of parasites have been found attacking 55 per cent of the eggs. An additional 5 per cent fail to hatch. Five species of larval parasites accounted for an average of 9 per cent of the mortality of the larvae. Woodpeckers play an important part in control, especially in heavily infested trees. In outbreak periods mortality of larvae from eggs laid in healthy trees is the major regulating factor.

Since the borer can only multiply in weakened trees and can only reach outbreak proportions in such host material, measures which tend to promote host vigour would appear to be the most satisfactory means of control.

Experiments with DDT against the adults indicated its value in protecting susceptible shade trees from borer attack. The adults die in from 24 to 48 hours after an exposure of one-half hour to surfaces sprayed with DDT at 1 to 2 pounds per 100 gallons. Trees can be protected from attack by two thorough applications of DDT at 10 pounds per 100 gallons. The first application should take place just before borer emergence, about June 20, the second about three weeks later. Spraying should be accompanied with measures to improve vigour.

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The North American Allies of *Hylobius piceus* (De Geer) (Coleoptera: Curculionidae)[1]

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While investigating the biology of the North American species of *Hypomolyx*, field workers in Manitoba found a vestigial, or short-winged, and a long-winged form under apparently identical conditions in about equal numbers. Although biological differences were not then apparent, there was doubt as to whether they were dealing with one dimorphic species or with two distinct species. A search for morphological characters brought to light numerous differences between the two forms, supporting the view that two species were present. These differences, a description of the previously unrecognized species, and notes concerning the status of the genera *Hylobius* and *Hypomolyx* are reported below.

Hylobius Germar

Hylobius Germar, 1817, Mag. Ent. 2: 340 (name validated); Schoenherr, 1826, Curculionidum Dispositio Methodica 4: 170 (described and type designated); Leconte, 1876, Proc. Amer. Philos. Soc. 15: 140; Blatchley and Leng, 1916, Rhynchophora of North Eastern America, p. 186; Dalla Torre, Schenkling and Marshall, 1932, Coleopterorum Catalogus 122: 6; Buchanan, 1934, Proc. Ent. Soc. Washington 36: 252.

Hypomolyx Leconte, 1876, Proc. Amer. Philos. Soc. 15: 139; Bedel, 1882, Bull. Séances Soc. Ent. France, p. CLXXIII (a synonym of *Hylobius*); Blatchley and Leng, 1916, Rhynchophora of North Eastern America, p. 187; Reitter, 1923, Wien. Ent. Zeit. 40: 21 (a subgenus of *Hylobius*); Dalla Torre, Schenkling and Marshall, 1932, Coleopterorum Catalogus 122: 7 (a subgenus of *Hylobius*).

The genus *Hylobius* as named by Germar (1817, p. 340) included two species, *Rhynchaenus pineti* Fabr. and *R. abietis* L. Nine years later Schoenherr (1826, p. 170) characterized the genus and designated *pineti* as the type species. Leconte evidently was not familiar with the European species *pineti*; consequently, he (1876, p. 139) described the genus *Hypomolyx* for the North American species *Hylobius pinicola* (Couper). Bedel (1882, p. CLXXIII) then made *pinicola* a synonym of *pineti*, and pointed out that since the type species of both *Hylobius* and *Hypomolyx* was *pineti*, Leconte's name *Hypomolyx* could not stand. Later, Bedel (1884, p. 95) placed both *pinicola* and *pineti* in synonymy under *Curculio piceus* DeGeer. Subsequent writers have followed Bedel's note of 1884, but have overlooked his note of 1882; as a result, Leconte's name *Hypomolyx* has been used for the "Holarctic" species *piceus*, and Germar's name *Hylobius* for the remainder of the genus. Although the present writer's observations indicate that the European *piceus* and the North American *pinicola* are taxonomically distinct, they most certainly are congeneric; consequently, the name *Hylobius* Germar, with *Rhynchaenus pineti* Fabr. (=*Curculio piceus* DeGeer) as the type species, must replace *Hypomolyx* Leconte.

In order to determine whether the group of species formerly placed in *Hylobius* (the allies of *abietis*) should have a new generic name, all accessible species in the *Hylobius-Hypomolyx* complex were examined. Particular attention was given the characters used by Leconte to separate the two groups, such as: body outline, coarseness of the anteocular grooves, postocular lobes, emargination of the prosternum, and presence or absence of femoral spurs. Special attention was also given the shape and sculpture of the pronotum, used by

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Reitter (1923). It was found that *albosparsus* Boh., *piceus* (DeGeer), *pinicola* (Couper), *warreni*, n. sp., and perhaps *verrucipennis* Boh. could be grouped rather conveniently on the basis of pronotal shape and sculpture, and absence, or near absence, of femoral spurs. It was also possible to group *abietis* (L.), *haroldi* Faust, *montanus* Kono, *pinastri* (Gyll.), *transversovittatus* Goeze, *congener* (Dalla Torre), *pales* (Herbst), and *radicis* Buch. on the basis of pronotal shape and sculpture, and presence of femoral spurs. Three species exhibit combinations of characters that make them appear intermediate between these two groups. For example: *alpheus* Reiche has the pronotum similar in size and shape to that of *abietis*, but the femoral spurs are reduced to small ridges as in many specimens of *warreni*; *exsculptus* Roel. has a pronotum similar in size and shape to that of *piceus* but lacks the lateral impressions, the femoral spurs are also absent; *galloisi* Kono has a pronotum rather similar to that of *piceus*, but has small femoral spurs. Also, the femoral spurs of *haroldi* and *montanus* of the *abietis* group are reduced in size, often appearing only as small ridges. Observation of the above-named species, approximately one-third of the known representatives of the complex, indicates that a division into two or more genera or subgenera, based on any one character or combination of characters is impossible. The intergradation of supposed generic characters found in the species examined will, in all probability, only be exaggerated by examination of the other representatives of the group.

Hylobius pinicola (Couper)

Figs. 1, 3, 5, 7, 12-14

Curculio pinicola Couper, 1864, Trans. Lit. Hist. Soc. Quebec, n. s., 2: 65.

Hylobius pinicola, Couper, 1864, Trans. Lit. Hist. Soc. Quebec, n. s., 2: 149; Couper, 1865, Trans. Lit. Hist. Soc. Quebec, n. s., 3: 32; Provancher, 1877, Petite Faune Entomologique du Canada, 1: 515; Bedel, 1882, Ann. Ent. Soc. France, series 6, 2: CLXXIII (a synonym of *pineti*).

Hypomolyx pinicola, Leconte, 1876, Proc. Amer. Philos. Soc. 15: 139.

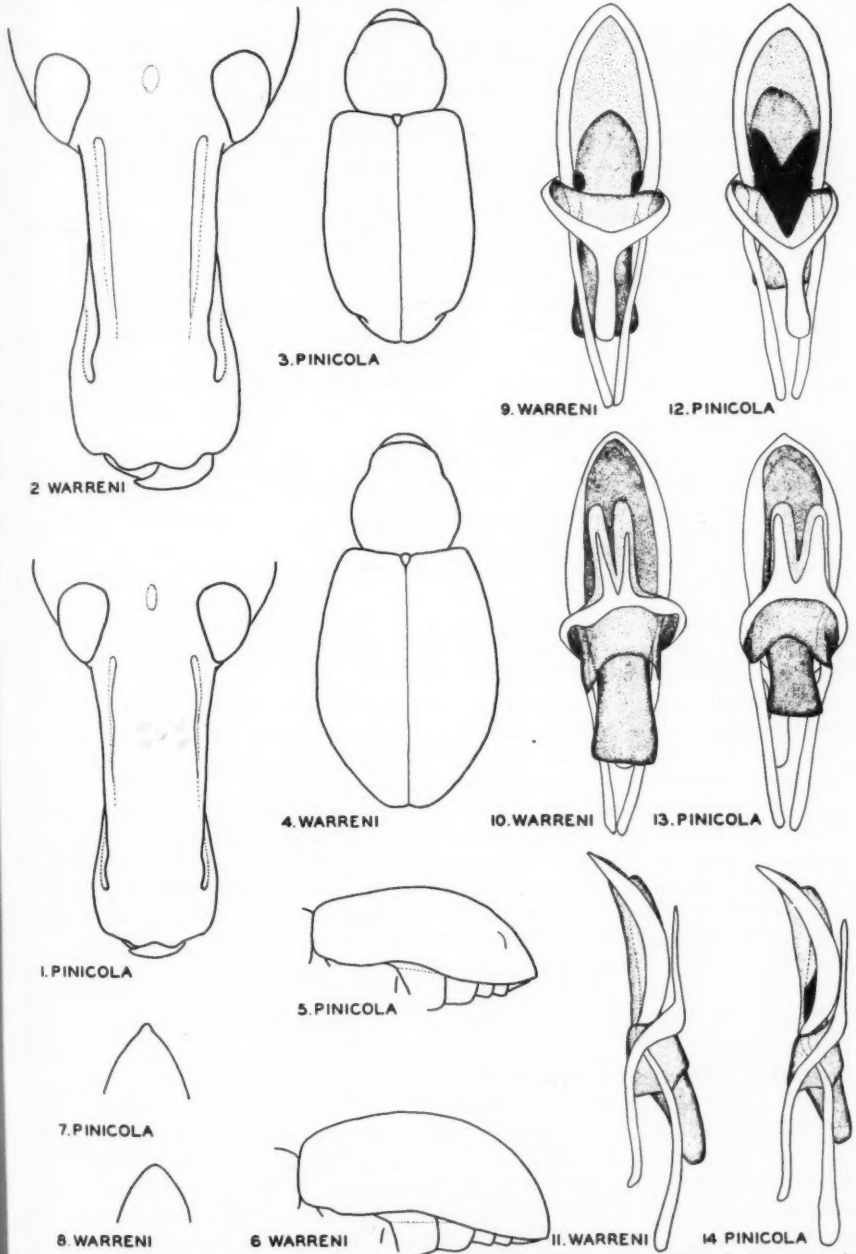
Hylobius heros Leconte, 1850, *In* Agassiz, Lake Superior: Its Physical Character, Vegetation, and Animals, p. 233 (nomen nudum); Couper, 1865, Trans. Lit. Hist. Soc. Quebec, n. s., 3: 33 (cited as a synonym of *pinicola*); Leconte, 1876, Proc. Amer. Philos. Soc. 15: 139 (cited as a synonym of *pinicola*).

Hylobius pineti, 1882, Bedel, Ann. Soc. Ent. France, hors serie, 6: 95 (a synonym of *piceus*).

Hypomolyx piceus, Blatchley and Leng, 1916, Rhynchophora of North Eastern America, p. 188; Lambert, 1944, Canada Dept. Agr. Div. Ent. For. Ins. Surv., Rept. for 1943: 23 (biology); Leech, 1944, Canada Dept. Agr. Div. Ent. For. Ins. Surv., Rept. for 1943: 66 (biology); Daviault and Lambert, 1946, Canada Dept. Agr. Div. Ent. For. Ins. Surv., Rept. for 1945: 23-24 (biology); Daviault, 1949, Forêt et Conserv. 1: 96-99 (biology).

The North American representatives of the *piceus* group were formerly treated as one species and considered synonymous with the widely distributed Eurasian species *piceus*. When two North American species were recognized by the writer, the available Eurasian specimens (19 from Finland, 3 from Switzerland, and 4 from Austria) were compared with them. Characters of the long-winged form corresponded very closely to those of the European specimens, but differed consistently in several respects. These differences, summarized in the key below, are not great and become conspicuous only when series are examined. Evidence obtained from the available material suggests that the long-winged North American form, *pinicola*, and the Eurasian form should be recognized as distinct taxonomic entities. Although it appears improbable at this time, the clinal intergradation of characters in specimens from the area between northwestern Canada and Europe could occur, thereby indicating that *pinicola* and *piceus* should be recognized as subspecies rather than species.

In addition to the differences mentioned below in the key, *pinicola* is slightly smaller (11.3-14.3 mm. long, averaging 12.5 mm. in 50 specimens, compared to



Figs. 1-2. Anterior aspect of female rostrum of *Hylobius* spp. 1, *pinicola*; 2, *warreni*.
Figs. 3-4. Dorsal aspect of male outline of *Hylobius* spp. 3, *pinicola*; 4, *warreni*.
Figs. 5-6. Lateral aspect of male outline of *Hylobius* spp. 5, *pinicola*; 6, *warreni*.
Figs. 7-14. Male genitalia of *Hylobius* spp. 7, *pinicola*, outline of tip; 8, *warreni*, outline of tip; 9, *warreni*, ventral aspect; 10, *warreni*, dorsal aspect; 11, *warreni*, lateral aspect; 12, *pinicola*, ventral aspect; 13, *pinicola*, dorsal aspect; 14, *pinicola*, lateral aspect.

12.0-15.3 mm., averaging 13.7 mm., in 26 specimens of *piceus*), and the general body colour appears grayish with indefinite, often confluent, patches of white or pale yellow spots (formed by slender scales). In *piceus* the colour is black with small, rather definite yellow spots. The anterior face on the basal half of the rostrum is more coarsely sculptured with the punctures largely confluent in *pinicola*; in *piceus* these punctures are usually smaller and well defined. The general surface of the pronotum and elytra is more finely sculptured in *piceus*.

The hosts for *pinicola* include eastern larch and white spruce. Black spruce and balsam fir are also listed, but may refer only to perching records.

A specimen definitely labeled as the type of *Curculio pinicola* Couper could not be located during this study, and may never have been designated. There were no specimens labeled as the type, or bearing a date before 1864, in either the Quebec Provincial Museum Collection or in the collection at McGill University, where most of Couper's collections are. However, Couper (1865, p. 32-33) published the following note under the name *Hylobius pinicola*, the year after the original description appeared:

"I remarked when the above was published that another of the same size was found in Western Canada, but with marked difference of elytral characters. I had not the western insect to compare with my Quebec specimen. However, I sent the latter to Dr. LeConte, who informs me that 'it is a good species allied to H. arcticus of the other continent.' He says 'he had it previously from Lake Superior, in Agassiz's Work.'

"This insect is therefore H. heros of Dr. LeConte's manuscript, and H. pinicola as cited above. However, I now leave it in the hands of the talented author of the Catalogue of N. A. Coleoptera."

From this note it is evident that his specimen (singular), presumably the one he recognized as the type, since his description was based on more than one example, was sent to Leconte. Because of the knack Leconte had for acquiring type specimens, it is presumed that this specimen was kept in his collection. At present, there is one specimen in the Leconte Collection, without locality label or other indication of origin, bearing in Leconte's hand the name "*Hylobius pinicola* (Couper)." Under the circumstances this specimen is recognized as the type of Couper's species. The characters of the rostrum and vestiture as described by Couper match those of this specimen, and, as observed by Dr. Darlington, the flight wings are long and folded.

Hylobius warreni, new species

Figs. 2, 4, 6, 8-11

Male.—Length 13.2 mm. (paratypes 11.7-14.4 mm., the average 13.0 mm.); body colour very dark brown to blackish, clothed with white to pale yellow hair and slender scales, the scales forming irregular, small, pale yellow spots on the elytra.

Rostrum about equal in length to or a little shorter than the pronotum; 2.4 times as long as wide (from 2.4 to 2.5 times as long as wide in paratypes; the length was measured from the upper level of the eyes to the apex of the rostrum); punctation dense on basal two-thirds, a little coarser than in *pinicola*, and impressed into about three indefinite longitudinal ridges; head more coarsely punctured and the interocular fovea a little larger than in *pinicola*; vestiture on rostrum and head almost white, a little longer than in *pinicola*. Pronotum somewhat variable in outline and sculpture, but more coarsely sculptured than in most specimens of *pinicola*, the punctures averaging coarser and closer and the vestiture longer; the hairlike setae about twice as long as the diameters of the punctures.

Elytra with sides (Fig. 4) and sutural profile (Fig. 6) more strongly arcuate (compare Figs. 3 and 5) and the strial punctures smaller than in *pinicola* (these differences evident in only about 75 per cent of the available specimens); apical umbones undefined; sculpture of interspaces, and vestiture, similar to those of *pinicola* except the patches of scalelike setae smaller and more definite. Venter essentially as in *pinicola*, the differences appearing inconsistent, although the median sulcus on the first visible abdominal segment usually much narrower and deeper. Hind (metathoracic) wings very short, not extending beyond the posterior margin of the first visible ventral segment of the abdomen. Genitalia as figured (Figs. 9-11).

Female.—Slightly larger than the male, the length varying from 12.0 to 15.1 mm., the average 13.7 mm.; head, thorax, and elytra indistinctly more finely sculptured; rostrum a little more slender, 2.5-2.6 times as long as wide (2.7 times in two specimens); sexual differences of pygidium as in *pinicola*; otherwise similar to the male.

Type Locality.—Clear Lake Trail, Riding Mountain National Park, Manitoba.

Hosts.—(?)*Abies lasiocarpa*, (?)*A. balsamea*, *Picea glauca*, (?)*P. mariana*, *Pinus contorta*, *P. strobi*, and *P. sylvestris*.

Type Material.—The male holotype was collected at the type locality on May 18, 1912, by J. M. Swaine; the female allotype was taken in Gaspé County, Quebec, on Aug. 5, 1933, by E. B. Watson. The 77 paratypes were collected as follows:—*Alberta*: Cold Lake, July 5, 1949 (A 998); Colinton, from White Spruce; Strachan, June 9 and Aug. 17, 1953. *British Columbia*: Golden, from Alpine Fir; McLeode Meadows in Kootenay Park, July 15, 1936, from Lodgepole Pine by K. Graham. *Manitoba*: Pine Falls, June 16, 1948, from White Spruce (W-284); Riding Mountain National Park, 1952 and 1953, from White Spruce by G. L. Warren; and Wasagaming, Sept. 17, 1951, from White Spruce. *New Brunswick*: Nashwaaksis, May 10, 1935, by C. C. Smith. *Nova Scotia*: Little River, Sept. 20, 1954 (W54-3753); and Manchester, July 13, 1954, from White Spruce. *Ontario*: Chapleau, Sept. 2, 1948 (S48-6373); Cochrane, June 29, 1948, from Balsam Fir (S48-1803); and Moose Factory, June 15, 1949, by D. F. Hardwick. *Quebec*: Anse St. Jean, July 6, 1939 (3800); Baie Comeau, July 9, 1936, from Black Spruce by L. Daviault; Baie St. Paul, Aug. 7, 1947 (39617-B); Cascapedia, Aug. 20, 1935, by C. C. Smith; Gaspé County, July 27, and Aug. 5, 1934, by E. B. Watson; Islets Caribou, July 9, 1943 (26189-B); Laniel, June 3, 1932, by H. S. Fleming; Macamic, June 16, 1939 (534); Maniwaki, Sept. 11, 1943 (26318-D); Parke Reserve, Aug. 3, 1936, by A. R. Gobeil; Rivière Musquorro, July 26, 1929 (1200-A); Sanmaur, June 30, 1939 (276A); St. Vianney, Sept. 3 (7677C), and Sept. 6, 1938 (7678B); and Trois Pistoles, June 25, 1946 (35294-A).

Other material examined, not included in the type series, include specimens from the following localities:—*Maine*: Bridgewater, Danforth, Rangeley, Seboomook, St. Francis, and Sorrento. *Michigan*: Marquette. *New York*: Raybrook. *North Carolina*: Black Mountain.

The holotype, allotype and some paratypes are in the Canadian National Collection; other paratypes are in the collections of the Museum of Comparative Zoology and the U.S. National Museum.

This species is superficially very similar to *pinicola*; in some cases individual specimens are recognized only with difficulty unless the hind wings or male genitalia are examined. However, it may be distinguished from *pinicola* by the following characters: the average size slightly larger; rostrum stouter, and more noticeably dilated distally (Fig. 2; cf. Fig. 1); basal portion of rostrum, head, and

pronotum tending to be more coarsely sculptured, with vestiture lighter in colour and distinctly longer; elytra with the sides and profile of the suture more strongly arcuate in most specimens (variable), the apical umbones not apparent (very prominent in *pinicola*, as indicated in Figs. 3 and 5), and interspaces tending to be more coarsely sculptured; hind wings less than one-half as long; median impression on first visible abdominal segment tending to be more narrowly impressed (variable); and male genitalia (Figs. 9-11; for terminology see Wood, 1952) with apex of aedeagus (median lobe) blunt, the anterodorsal margin of the gonocoxites (tegmen) conspicuously bisinuate, and the processes on the posterodorsal margin of the gonocoxites longer and more slender; a darkly pigmented median plate within the aedeagus not visible (compare Figs 12-14).

A certain degree of host selection was indicated by the available records. The 34 series of *pinicola* with host data, from 32 localities, were recorded as follows: eastern larch, 19; white spruce, 10; black spruce, 3; and balsam fir, 2 (definite breeding records included larch and white spruce). The 56 series of *warreni* with host data, from 14 localities, were recorded as follows: white spruce, 40; black spruce, 1; balsam fir, 1; alpine fir, 1; scotch pine, 8; white pine, 5; and lodgepole pine, 1 (definite breeding records included white spruce, white pine, and scotch pine).

The principal differences between the two North American species and the Eurasian species with which they have been confused are summarized in the following key.

Key to Species

1. Rostrum rather stout, less than 2.6 times as long as wide, noticeably wider distally (Fig. 2); apical umbones of elytra obscure or entirely undefined; metathoracic wings short, not extending beyond posterior margin of first visible abdominal sternum; male genitalia (Figs. 8-11) with apex of aedeagus blunt, the anterodorsal margin of gonocoxites conspicuously bisinuate, and lacking a darkly pigmented median area within the aedeagus ..... *warreni*, new species

   Rostrum slender, more than 2.9 times as long as wide, not wider distally (Fig. 1); apical umbones of elytra prominent; metathoracic wings long, extending well beyond elytral apex; male genitalia with apex of aedeagus acutely pointed, the anterodorsal margin of the gonocoxites evently rounded, and a pigmented median triangular or V-shaped area within the aedeagus visible from the ventral aspect 2

2. Pronotum brownish-black, the surface minutely reticulate and dull, the punctures coarse, close, and usually with their posterior or lateral rims elevated, the hairlike setae longer, averaging about twice as long as the diameter of the punctures; elytral interspaces more coarsely sculptured, each puncture with the anterior margin raised; the hairlike setae on elytra lighter in colour and longer, averaging about half as long as the width of the interspace; male genitalia (Figs. 7, 12-14) with ventral pigmented plate of aedeagus with both anterior and posterior margins sharply V-shaped; a North American species ..... *pinicola* (Couper)

   Pronotum black, the surface smooth and shining, the punctures finer and rather sparse, rarely with their posterior or lateral rims feebly elevated, the hairlike setae shorter, averaging about one and one-half times as long as the diameter of the punctures; elytral interspaces more finely sculptured, the anterior margin of each puncture weakly or not at all elevated; the hairlike setae on elytra darker in colour and shorter, averaging about one-fourth as long as the width of the interspace; ventral pigmented plate of aedeagus more or less triangular, the anterior margin less sharply pointed and the posterior margin very broadly U-shaped; a Eurasian species ..... *piceus* (DeGeer)

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Three Useful Insect Cages[1]

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Three types of cages, suitable for rearing potato-infesting aphids on whole plants, parts of plants, and excised leaves, have been developed during aphid investigations at the Fredericton laboratory. These cages have been used in the greenhouse and insectary with the four potato-infesting aphids *Myzus persicae* (Sulz.), *Macrosiphum solanifolii* (Ashm.), *Aphis abbreviata* Patch, and *Aulacorthum solani* (Kltb.).

Copper Screen Cage

A copper screen cage (Fig. 1) has been used to rear aphids on potted potato plants. A wooden frame 36 inches high, 18 inches wide, and 36 inches deep (the depth of the greenhouse bench) is covered with 36-mesh copper screening. The cage has a hinged door on the front and a plywood bottom. This cage has been used to rear potato-infesting aphids throughout the year in the greenhouse (MacGillivray, 1955). A leafhopper on corn, *Dalbulus maidis* (DeL. and Wol.), has also been reared successfully in this cage.

Organdy Cylinder Cage

Organdy cages (Fig. 2, D) have been used to confine aphids to single,

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excised potato leaves. One end of a cylinder of "permanent" organdy is attached with cellulose tape to a ring of cardboard of the same diameter and 1.5 inches high. The other end of the organdy cylinder is gathered and sewed together. Before the cardboard ring is attached, it is dipped in a 0.1 per cent solution of mercuric chloride to prevent fungous growth, dried, and then dipped in paraffin wax to protect it from water damage. The cardboard ring is made to fit the size of the pot used. If the rings are smaller, sponge-rubber weather stripping is used to fill in the space. Generally, with pots four inches in diameter, cages about six inches high are used.

The pot is filled with damp moss packed around a vial. The moss is covered with green blotting paper (Fig. 2, A) to facilitate the finding of cast skins. The vial (Fig. 2, B) is filled with water and stoppered with a bored cork (Fig. 2, C). The stem of an excised potato leaf is severed under water to eliminate air-blocks and then inserted into the vial of water through the bored cork and covered with the organdy cage.

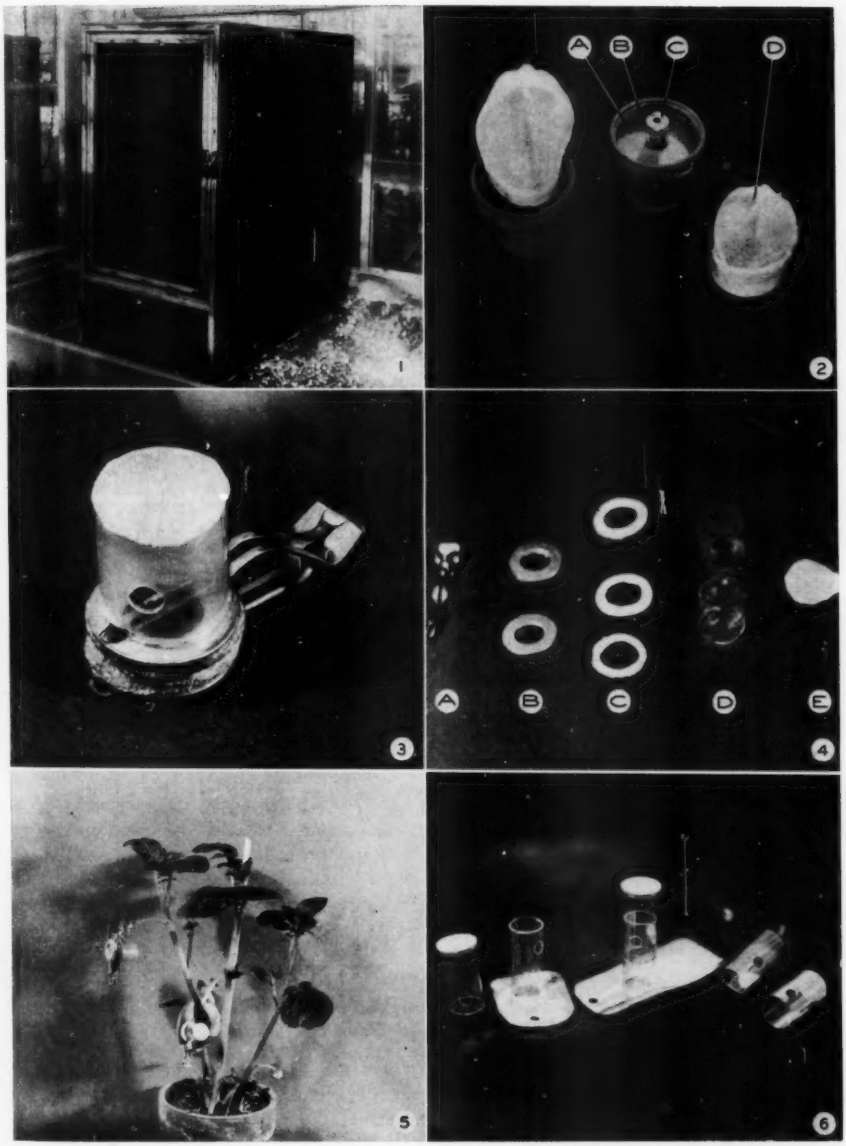
All stages of the aphids and their cast skins are easily found when this cage is used. The leaves are renewed periodically as required. Usually, when more than 30 aphids are placed on a leaf, the leaf must be renewed every three days. When single plants are used, the leaf lasts about a week. Potted plants may also be used with this cage, the size of the plant determining the size of the cage to be used. Cages more than six inches high require support to keep the organdy upright. Twist-ems (W. H. Perron, 91 Labelle Boulevard, L'Abord-a-Plouffe, Quebec), used for tying plants, give adequate support.

Clip Cage

On a whole plant a single aphid is difficult to find since the aphid may wander to different parts of the plant. Cast skins may be overlooked and nymphs may be scattered over several leaves. Time may be lost in searching for the aphid, cast skins, and nymphs and sometimes these may not be found. To overcome these difficulties in investigations on individual aphids reared on whole plants, various leaf cages were used. The manipulation of most of these was tedious.

Kennedy and Booth (1950) described a single-leaf or reproductive cage useful in aphid studies. Bonnemaison (1950) described a cage he used when studying aphids on a confined area of leaf tissue. None of these cages is adaptable to the needs of the Fredericton laboratory. Maramorosch (1951) described a cage he used in insect-vector studies. This is simply constructed, easy ot manipulate, and inexpensive. Features of Maramorosch's cage and one previously constructed by Mr. L. A. Dionne at the Fredericton laboratory have been combined.

The cage (Fig. 3) is made of two small cylinders of polystyrene plastic centrifuge tubes (Central Scientific Company of Canada Limited, 7275 St. Urbain Street, Montreal 14, Quebec) 1.5 cm. in diameter, as described by Maramorosch (1951), glued to a metal hair clip (Lady Ellen Arched Klippies, The Kaynar Company, New York, N.Y.). The metal hair clip (Fig. 4, A) is 4.5 cm. long. It is 0.8 cm. wide at the spring end and tapers to a point at the other end. Aluminimum washers (Fig. 4, B) with an opening 1.0 cm. in diameter are glued to the inner surface of each prong of the clip. Two layers of sponge chamois are glued to one metal washer and one layer to the other. Each layer of sponge chamois (Fig. 4, C) is 0.01 cm. thick and has an opening 1.0 cm. in diameter. Household Cement (Canadian Industries Limited, Box 10, Montreal, Quebec) is used as an adhesive.



Figs. 1-6. 1, Capped screen cage. 2, Organdy cylinder cage; A, blotting paper; B, glass vial; C, bored cork; D, organdy cap. 3, Clip cage. 4, Clip cage parts; A, metal hair clip; B, aluminium washers; C, sponge chamois washers; D, sections of centrifuge tube; E, organdy disc. 5, Intact potato leaves bearing clip cages. 6, Maramorosch cage, showing section of centrifuge tube attached to strip of cellulose nitrate.

The centrifuge tubes are cut into 1.5-cm. lengths. Two of these sections (Fig. 4, D) are used for each cage, one section fitting inside the other. To procure the proper diameter for the inner cylinder, it is necessary to slit the tube lengthwise, overlap the edges, and glue them with acetone. A disc of "permanent" organdy (Fig. 4, E) is glued with acetone over one end of the outer tube. The inner tube is glued with acetone to the upper surface of the prong of the hair clip and to the aluminium washer that bears the two layers of sponge chamois. On one side of each cylinder, holes 0.5 cm. in diameter are made with a paper punch and when apposed allow for the introduction of aphids.

When the cage is used it is clipped to the leaf, the leaf resting between the sponge-chamois washers (Fig. 5). The aphids may be introduced through apposed holes in the tubes and allowed to find their way to the leaf surface. A slight turn of the outer tube blocks off the holes. As nymphs are sensitive to handling, when they are used it is preferable to introduce an adult and allow her to deposit a nymph on the leaf and then remove the adult.

In this cage the aphids develop and reproduce readily. The cages are light in weight, easy to manipulate, and suitable on intact and excised leaves.

Maramorosch (1951) attached the inner centrifuge tube to a strip of cellulose nitrate over an opening covered with plastic screen (Fig. 6). In this cage the insects are easily transferred from plant to plant, but in the studies at Fredericton it was found that first-instar nymphs could go through the screen.

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A Note on the Circulus as an Adhesive Organ in Some Pseudococcidae

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Adhesive or climbing organs in the form of empodia or pulvilli between the tarsal claws are common structures in Hymenoptera, Diptera, Hemiptera and other orders (Weber 1933). A more unusual type consisting of a small oval sac on the distal end of the tibia of the prothoracic and metathoracic legs of the reduviid *Rhodnius prolixus* Stål. has been described by Gillett and Wigglesworth (1932).

Recently it has been observed that the circulus structure of some Pseudococcidae performs an adhesive function at certain stages in their life cycles. Attention was first called to this fact when it was noticed by one of us (E.M.) that nymphs and adults of the mealybug species *Planococcus citri* (Risso), *Pseudococcus maritimus* (Ehrh.), *Pseudococcus adonidum* L., *Pseudococcus gahani* Green, *Phenacoccus gossypii* Twns. and Ckll., and *Phenacoccus solani*

Ferris showed varying abilities to climb and descend the glass walls of the one gallon jars used for routine laboratory production of encyrtid and aphelinid parasites. Ferris and Murdock (1936) and Ferris (1950) have pointed out that, although of unknown function, the circulus is a definitive structure of the family Pseudococcidae which appears typically in stained cuticular preparations as a faint weakly sclerotized ring usually across the ventral intersegmental fold between the—morphologically—fourth and fifth abdominal segments. Some mealybug species have more than one circulus, while in a few it is lacking. When present it is stated to occur in all stages of the female, with the enclosed area described as being free of pores and setae. In living specimens the circulus frequently shows as a rather prominent tumid area without wax but it is often retracted and invisible. The above workers investigated the organ histologically and otherwise in *P. maritimus* and concluded that "in view of the entire absence of any external evidence of functional activity and considering the sequence of stages which appear in the organ itself, it may be suggested that it is actually a glandular structure, the contents of which are discharged internally. Whether this activity occurs in every instar or whether it is restricted only to the last stage and may have some connection with egg production remains to be determined."

Our observations in the laboratory with the six species of mealybugs listed above have definitely established that all species except *Ph. solani* use the circulus as an adhesive organ although its effectiveness in this capacity seems rather limited. Furthermore, such use is apparently restricted to the mature female stage, the first three nymphal instars being able to ascend or descend with ease, by the usual leg actions, even clean perpendicular glass surfaces. Since the final moult of the female in all species takes place when the size range is between 1.5 and 2.0 mms. it is probable that the use of the structure in an adhesive capacity occurs only during the latter half of the mealybug growth.

The circumstances under which the circulus is brought into function may be observed by placing a few mature specimens of an active species such as *P. adonidum* on a citrus fruit or at the bottom of a small glass container. Most individuals ascend the sides of the container to various heights, and in so doing the circulus is seen to be periodically extended so as to adpress it firmly to the side walls. If at this moment a specimen is viewed laterally under a binocular microscope the ventral abdomen is observed to be completely free of the substratum except at the mesal portion of segments four and five where the circulus forms the summit of a small cone. While the organ performs this holding function various legs are moved in an exploratory manner until the claws and associated "tenent hairs" make adequate purchase on the substratum to permit forward motion again. These exploratory leg movements may take place in various directions since attachment by the circulus allows the mealybug to pivot at this point and rotate the body through a fairly wide arc. All forward movement is therefore by leg action and the circulus definitely does not propel the mealybug forward, as do the eversible abdominal "pygopodia" of some coleopterous and dipterous larvae (Wigglesworth 1950). It is probable that the spatulate tarsal and claw setae present in these mealybugs are types of adhesive organs classed as "tenent hairs," and thus used in movements on surfaces such as clean glass, whereas the claws alone are adequate for rougher surfaces. These setae number four per tarsus in the above *Planococcus* and *Pseudococcus* species, but only two per tarsus in the *Phenacoccus* spp. Ferris (l.c.) gives good illustrations of some of these setae, which he describes as "digitules."

There are indications that the circulus is only brought into function when the normal climbing organs begin to fail. But this action is often unsuccessful

and under observation larger mealybugs frequently fall off glass or even more normally encountered substrata in the form of fruit and lower leaf surfaces of citrus. This stabilizing action of the circulus has also been seen to occur under conditions other than locomotor as when a mature female settles at a point for egg mass formation or mouth part insertion for further feeding.

The mechanism causing extrusion of the circulus is not known. Ferris and Murdock (l.c.) suggested that the organ is secretory with the contents discharged internally. The fluids noted by these workers in the dermal cells of the structure may enable the circulus to act as a sucker, although an adhesive function also implies passage of small amounts of fluid to the exterior. The clear, wax-free surface of the circulus shows a colouring typical of the body fluids of some mealybugs (e.g. *P. gahani*), and it is possible that extrusion is produced by body muscle contractions with transfer of haemocoele fluids to the abdomen.

Dispersive movements by mature female mealybugs over the host plants prior to egg mass formation are known to be characteristic of certain species. Smith and Armitage (1931) and DeBach (1949) state that the species *P. gahani* and *P. adonidum* tend to congregate on trunks whereas *Pl. citri*, *P. maritimus* and *Ph. gossypii* usually deposit egg sacs at the points where feeding is completed. The use of the circulus in climbing and descending citrus fruit and leaves has been noted during current laboratory observations and there can be little doubt that the organ is so employed in host tree movements under field conditions. Although there are obvious qualitative differences in the walking and climbing capabilities of the foregoing six mealybugs, the circulus is only one of various organs taking part in the mechanics of these activities and therefore establishment of correlations between such activities and the degree of circulus development is likely to be difficult. The organ appears equally well developed in all above species except *Ph. solani*, which we have not seen to use the circulus, and which in the mature stage cannot ascend perpendicular glass surfaces. The reduced size of the circulus in *Ph. solani* may be associated with the surface and subterranean habitats of that mealybug in contrast to the typically aerial habitats of the other species, yet the briefest review of the mealybugs described in the Atlas of Scale Insects of North America demonstrates the difficulties in generalizing on these lines. We conclude that the circulus when present may well function as a rudimentary adhesive organ in most Pseudococcidae but this is not necessarily its sole function.

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